ANTARCTIC GLOSSOPTERIDS: CLARIFYING AND COMPARING REPRODUCTIVE STRUCTURES

BY

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ABSTRACT

Glossopterid reproductive structures, both impressions and permineralizations, have been known from Antarctica for decades, but little detailed work has been done on them to date. Impression fossils from the Central Transantarctic Mountains reveal that at least four genera of reproductive organs are present on the continent. *Plumsteadia* is a genus of multiovulate megasporophylls found on all Gondwanan continents and distinguished by tightly compacted ovules surrounded by a wing which contains a row of ovules at its base. Numerous specimens of *Plumsteadia ovata* Kyle add additional information on anastomosing venation in the sporophyll and a fluted margin on the wing to the species description. A new species of *Rigbya*, an ovulate organ, is characterized by the laminar appearance of the cupules/scales and a crenate margin at the apex of the cupules. *Eretmonia singulia* sp. nov., a microsporangiate structure, is distinguished by the terminal attachment of a single sporangium on a dichotomizing stalk rather than a whorl of sporangia as found in other species. Finally, *Arberiella inflectada* sp. nov., a cluster of pollen sacs, includes microsporangia with a distinctive, recurved base. These impression genera are found across Gondwana, suggesting that Antarctica, with its central location in the supercontinent, was a bridge for the distribution of glossopterid genera from one Gondwanan continent to another. The relative scarcity of information garnered from these impression specimens presents a conservative estimate of the diversity of the glossopterid clade, but information from Antarctica adds considerably to our knowledge of this group.

Permineralized reproductive structures have been known from Antarctica for the past four decades. No formal descriptions have been available for this material, however, leaving a gap in our knowledge of the glossopterid clade. *Lakkosia kerasata* gen. et sp. nov. is a multiovulate, megasporangiate structure found in silicified peat from the Late Permian Skaar Ridge locality in the Central Transantarctic Mountains. Ovules are borne in depressions on the adaxial surface of the megasporophyll and enclosed in thin strips of tissue that arises from the sporophyll. Transfusion tissue with scalariform wall thickenings is present in the sporophyll and may have acted as a storage or conducting tissue. In longitudinal sections of the ovules, the sclerotesta forms two appressed, hemispherical masses of lignified parenchyma cells which create the micropyle. Tissue of the sarcotesta overarches these parenchymatous masses, creating a chamber above the micropyle. *Lakkosia* is compared to previously described permineralized material from Antarctica, permineralized reproductive structures from the Bowen Basin of Australia, and impression material found in Antarctica.

Arberiella is an aggregation of pollen sacs associated with all the microsporangiate structures attributed to the Permian Glossopteridales. Microsporophylls are characterized by scale leaves (smaller leaves with similar morphology as *Glossopteris* leaves) that bear clusters of sporangia (*Arberiella*) at the end of pairs of pedicels. Late Permian permineralized specimens of *Arberiella* from the Central Transantarctic Mountains in Antarctica reveal that the pollen sac walls consist of two types of cells. Rectangular parenchyma cells form a tissue one to two

layers thick and constitute the majority of the sac wall. Lignified elongated cells are dispersed randomly among the parenchyma cells and probably correspond to striations on the surface of the pollen sac. This differentiation of cells in the pollen sac has not been described in any *Arberiella* species. No pollen sac is preserved in its entirety, but they appear to be bean shaped with a bulbous apex. Up to 12 pollen sacs were identified by the presence of aggregations of bisaccate pollen grains surrounded by remnants of pollen sac walls. *Arberiella schopfii* is most similar to the impression species *A. vulgaris*, but with the limited amount of information available from impression material, classifying the permineralized Antarctic specimens as *A. vulgaris* is premature. The simplicity of the pollen sacs does not suggest a specialized form of pollination, but rather that the glossopterids were wind pollinated. The morphology of these sporophylls is similar to that of pollen cones of other gymnosperms and most especially the Cycadales. The organization of glossopterid microsporophylls supports a gymnospermous affinity for the Glossopteridales.

A comparison of these new Antarctic taxa to species found on other Gondwana continents is provided to illustrate the diversity and geographic range of glossopterid reproductive structures.

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Chapter 1

Introduction to the *Glossopteris* plant and the Permian of Antarctica

1. The Permian World

The Permian period lasted from 299–251 Ma during which time the continents were grouped into two large landmasses known as Laurasia and Gondwana, which combined to form Pangea. Laurasia consisted of modern-day North America, Europe, and parts of Asia. Gondwana consisted of the continents of South America, Africa, India, Australia, New Zealand, and Antarctica. Two diverse floras covered these continents. In the Northern Hemisphere, the Early Permian landscape was similar to that of the Late Pennsylvanian with a transition throughout the Permian from Carboniferous coal swamp plants to a drier habitat with the pteridosperms and conifers that dominated the Mesozoic (DiMichele et al., 2001). Most of Gondwana was covered with several expanding and retracting ice sheets through much of the Late Carboniferous and Early Permian (Isbell et al., 2003; Fielding et al., 2008; Isbell et al., 2008). During maximum glacial extent, ice reached as far as the Congo Basin in Africa (Visser, 1997), the Paraná Basin in Brazil (Isbell et al., 2003), and to the northern margin of the Indian subcontinent (Veevers and Powell, 1987; Blakey, 2008). Ice covered southern and western Australia (Lindsay, 1997) as well as the majority of Antarctica (Isbell et al., 2008).

As the glaciers retreated braided river systems formed from glacial melt providing an environment in which plant colonization occurred (e.g., Isbell, 1991; Gupta, 1999; Gastaldo et al., 2005). The landscape became dominated by what has been known as the *Glossopteris* flora. While plants attributed to the extinct pteridosperm group Glossopteridales were dominant features of the landscape, they did not create a monogeneric landscape. Pteridophytes, conifers, and cycads were also components of this landscape (Walkom, 1922; Srivastava, 1954; Plumstead, 1964; Vieira et al., 2004). By the end of the Permian the ice sheets were gone and vegetation covered the planet from the equator to the poles.

2. *Glossopteris* Plant

The reconstruction of the *Glossopteris* "plant" is based on disarticulated organs found within the same deposit. The majority of the information on glossopterid organs comes from impressions, some compressions, and rare permineralizations. The mode of preservation of the majority of the glossopterid specimens (impressions) has only provided information on rough morphology. Rarely is anatomical attachment seen (e.g., Pigg and Taylor, 1993). *Glossopteris* Brongniart (Latin for "tongue-shaped") is the generic name for strap-shaped leaves with entire margins, a distinctive midrib consisting of several veins, and anastomosing secondary venation (Fig. 1; Brongniart, 1828). Other morphogenera have been assigned to the glossopterids based on similar morphology. *Gangamopteris* (McCoy, 1847) is most often associated with the glossopterids but is distinctive from *Glossopteris* by the absence of a midrib. *Gangamopteris* has been suggested as more common in the

Early Permian whereas *Glossopteris* is dominant in the Middle to Late Permian (McCoy, 1847; Retallack, 1980). Other leaf genera include: *Belemnopteris* with a chordate base (Pant and Choudhury, 1977), *Rhabdotaenia*, which has a distinct midrib but no anastomosing secondary venation (Pant, 1958), similar to primitive cycad leaves (Mamay, 1976), *Palaeovittaria* containing parallel veins with rare anastomoses (Pant and Verma, 1964), and *Euryphyllum* with veins radiating out from the petiole and rare anastomoses (Chandra and Singh, 1996). Leaves assigned to the glossopterids are so abundant in Permian rocks that *Glossopteris* is considered an index fossil for the Permian period. *Glossopteris* is found on all continents in the Southern Hemisphere and its presence there was some of the earliest evidence of continental drift (Wegener, 1924). Leaves are often found in leaf mats suggesting that *Glossopteris* plants were seasonally deciduous plants that shed their leaves in the fall, based on their occurrence in varved deposits (Plumstead, 1958a, Retallack, 1980). While the majority of *Glossopteris* leaves have been identified in Permian deposits, leaves assignable to the genus have also been found in Late Carboniferous (e.g., Rigby, 1966; Li and Yao, 1985) and Triassic (Fig. 2; Pant and Pant, 1987, Holmes, 1992) rocks. A couple of reports have found leaves with glossopterid morphology in the Jurassic (*Mexiglossa* Delevoryas and Person, 1975; Ash, 1981). Impression specimens indicate that the leaves were attached in a whorl to branches, but branching of the plant is unknown (Figs. 2, 3; Thomas, 1952; Pant, 1967; Holmes, 1992).

Numerous petrified or permineralized logs have been found in rocks that contain glossopterid leaves and other plant parts. A few accounts of anatomical

attachment have been recorded from permineralized specimens of *Glossopteris* (Pant and Singh, 1974; White, 1978; Pigg and Taylor, 1993), but the abundance and wood and leaves in the same deposits supports a probable association. This has led to most reconstructions of *Glossopteris* as a tree (Fig. 4; e.g., Pant and Singh, 1974; Gould and Delevoryas, 1977). The wood has been assigned to the morphogenus *Dadoxylon* Endlicher, which is defined as pycnoxylic wood with uni- to biseriate parenchymatous rays and tracheids with one to four rows of alternate circular bordered pits (Maheshwari, 1972). *Dadoxylon* is also considered a morphogenus associated with the Cordaites, a possible progenitor of the glossopterids (Schopf, 1976), as well as several other Paleozoic conifers. The morphogenus *Araucarioxylon* Kraus has also been attributed to the glossopterids (Retallack et al., 2007) and contains similar anatomy and morphology to *Dadoxylon* but has been utilized for Mesozoic woods rather than Paleozoic woods. Recent studies have suggested that both *Dadoxylon* and *Araucarioxylon* are illegitimate names for the wood assignable to this group and the appropriate morphogenus is still debatable (Philippe, 1993; Philippe and Bamford, 2008).

The rooting structure of the *Glossopteris* plant, *Vertebraria* (Royle, 1833 ex McCoy, 1847), is distinctive to the group, with alternating wedges of *Dadoxylon-Araucarioxylon*–type wood separated by air spaces (Schopf, 1965; Neish et al., 1993). The presence of an exarch actinostele and an endodermis has confirmed that *Vertebraria* is a root rather than a trunk or branching organ (Neish et al., 1993). The presence of a bifacial vascular cambium and secondary phloem has provided new

evidence of the anatomy of *Vertebraria*; however, there is not enough extraxylary tissue for comparison between glossopterid trunks to determine the anatomical diversity within the genus (Decombeix et al., 2009).

Both megasporangiate and microsporangiate structures attributed to the Glossopteridales have been found on all Gondwana continents (Table 1). The association of the reproductive structures is based on the abundance of the reproductive organs and *Glossopteris* leaves in the same deposit and similar morphology between the reproductive structures and the vegetative leaf. There are five genera of microsporangiate structures that are known, but these show few morphological differences. The most common microsporophyll is *Eretmonia*, which is described as a glossopterid scale leaf bearing a pair of pedicels with clusters of sporangia (du Toit, 1932). Genera with morphology similar to that of *Eretmonia* include *Squamella* (White, 1978) and *Glossotheca* (Surange and Maheshwari, 1970), which differ in the number of pairs of pedicels attached to the scale leaf. A second morphological type is *Nesowalesia* (Pant, 1977) which bears microsporangia in a cup-shaped structure. The sporangia attached to all microsporangiate genera show the same morphology—a thin-walled bean shaped structure with longitudinal striations running from the base to the apex of the sporangium. When these sporangia are found isolated in the matrix and unassociated with any scale leaf they are called *Arberiella* (Pant and Nautiyal, 1960).

Nearly 40 genera of megasporangiate structures have been described from across Gondwana ranging from leaf-like sporophylls containing numerous ovules to a

single scale leaf containing a single attached ovule (Table 1). Most reproductive specimens are classified into only a few form genera since not a wealth of information can be garnered from impression material. Localities in South Africa, Australia, and India have provided the most information on the diversity of glossopterid ovulate structures. A lack of exposure and collection availability in South America and Antarctica have resulted in less information on the glossopterids from these continents compared to the rest of Gondwana.

Multiovulate megasporophylls (e.g., *Scutum* Plumstead, 1952; *Plumsteadia* Rigby, 1962; *Dictyopteridium* Feistmantel, 1881) exhibit venation similar to *Glossopteris* with morphological variations in the margin of the sporophyll and the attachment of ovules (Fig. 5). In many impressions, the megasporophyll appears to be either attached to the midrib of a typical vegetative *Glossopteris* leaf or borne on a stalk in the axil of the left, supporting a glossopterid affinity of these morphotypes (Fig. 6). A second morphology that typifies some glossopterid reproductive structures is a small scale leaf bearing pairs of pedicels that terminate in a cluster of either micro- or megasporangia (Fig. 7). This morphological type is associated with the glossopterids based on similar venation and leaf shape of the scale leaf and *Glossopteris* leaves (e.g., *Lidgettonia* Thomas, 1958; *Eretmonia* du Toit, 1932). No *Glossopteris* leaf has been found in definitive association with this reproductive structure, but the presence of numerous *Glossopteris* leaves in the same matrix and the similar morphology between *Glossopteris* leaves and these scale leaves supports an affinity. A third type of ovulate reproductive structure associated with the

glossopterids consists of an axis bearing terminal dichotomizing stalks that each end in a cupule or scale leave with a single ovule attached at the base of the laminar structure (Fig. 8; *Rigbya* Lacey et al., 1975); the overall morphology appears fan like. This final type is considered glossopterid only on the presence of *Glossopteris* in the same matrix. The variety of morphological types of reproductive structures in the glossopterids illustrates that the diversity of the Glossopteridales is greater than that indicated by the vegetative structures of *Glossopteris* and *Vertebraria*, which are similar throughout Gondwana.

2.1 South African megasporophylls

The hallmark study by Plumstead (1952) generated a morphological interpretation that became the basis for studying glossopterid reproductive material throughout Gondwana for decades. Throughout her career Plumstead named six genera of multiovulate sporophylls (Table 1) but several of these genera no longer carry the name she instituted. The genus *Cistella* Plumstead was already occupied and was renamed *Plumsteadia* by Rigby (1969). *Lanceolatus* Plumstead and *Pluma* Plumstead are morphological variants of a previously described genus and, in her dissertation, Adendorff (2005) has proposed combining them into *Plumsteadia*, *Scutum*, and *Gladiopomum*. *Hirsutum*. *Scutum* Plumstead was described as a bisexual sporophyll with stamens surrounding a central cluster of ovules (Plumstead, 1958b). A recent examination of these specimens (Adendorff, 2005) has shown that instead of a bisexual structure, the sporophyll contained ovules surrounded by two wings, one which had been interpreted by Plumstead (1958b) as stamens.

Numerous other paleobotanists have expanded our knowledge of South African fructifications. In addition to the megasporophyll material described by Plumstead (1952, 1956a, b, 1958b) several authors presented work on cupulate-like material. Thomas (1958) described *Lidgettonia* as a glossopterid leaf with two rows of pedicels arising from the midrib; each terminated in four small leaves that formed what he described as a cupule. Further investigation of the genus revised the diagnosis to a scale leaf with pairs of pedicels terminating in cupules with ovules or ovule scars surrounded by a wing (Lacey et al., 1975). These investigators also designated new genera based on the number of pairs of pedicels attached to the scale leaf: one pair in *Rusangea*, two to four in *Mooia*, and *Lidgettonia* with two to 14 pairs of cupules. More recent studies (Anderson and Anderson, 1985; Adendorff, 2005) have suggested that the differences among these three genera are not enough to constitute separate genera and consolidated all specimens into *Lidgettonia*. Several multiovulate genera have been proposed by South African paleobotanists which have been consolidated into existing genera by further examination and study (e.g. *Scopus* and *Fetura* Benecke, 1976; Table 1).

Rigbya is unique and questionable glossopterid fructification with no attachment to *Glossopteris* and no morphological features similar to known glossopterid organs. The genus consists of a long petiole that dichotomizes several times ending in four to ten terminal scales in a fan shape, each bearing a single ovule. The genus is considered glossopterid based only on the presence of *Glossopteris* leaves in the matrix where material is found.

2.2 Indian megasporophylls

Numerous reports of glossopterid ovule-bearing structures from India indicate the presence of approximately 19 genera, some cosmopolitan across Gondwana and others distinctive to the Indian subcontinent (Table 1). Many of the genera are based on a few incomplete specimens (i.e., *Jambadostrobus* and *Venustostrobus* Chandra and Surange, 1977) and probably represent morphological variations of a larger morphogenus (i.e., *Plumsteadia*, *Scutum*, *Dictyopteridium*). Genera endemic to India and those absent from there indicate that the diversity of the Glossopteridales was not uniform across Gondwana. *Denkania* has been described as a scale leaf with 5–6 pedicels attached along the midrib, each terminating an uniovulate cupule (Surange and Chandra, 1971). This genus differs from *Lidgettonia* in not having pairs of pedicels along the midrib region. *Denkania* is also believed to be a uniovulate cupule while *Lidgettonia* is suggested to be a multiovulate cupule (Adendorff, 2005). *Denkania* differs from *Rigbya* in the loosely longitudinal attachment of ovules to the scale leaf. *Rigbya* has a fan-shaped arrangement with the scales associated in the same horizontal plane, which is not observed in *Denkania*. *Rigbya* has not been reported from India, supporting the conclusion that *Denkania* and *Rigbya* are not potentially the same genus. Several decades have passed since Indian material was examined and with new interpretations of glossopterid reproductive morphology presented in the last 20 years, specimens need to be reexamined for more accurate diagnoses.

2.3 Australian megasporophylls

The most consistent research on glossopterid fructifications has been in Australia since specimens were first observed there (Rigby, 1961). The earliest reports of reproductive material was based on microsporangia (Arber, 1905), but were not definitively classified as pteridosperm until megasporophylls were found. The most cosmopolitan Late Permian genera, *Plumsteadia*, *Dictyopteridium*, and *Scutum*, are found in eastern Australia (Rigby, 1962; White, 1963; McLoughlin, 1990a). Australia, like South Africa and India, also appears to contain endemic genera. The most prominent genus is the Late Permian *Austroglossa* from New South Wales, described as bearing ovules attached to a megasporophyll borne on a pedicel; there does not appear to be a marginal wing on the megasporophyll as seen in other genera (Holmes, 1974; Holmes, 1990). Another genus unique to the Late Permian of Australia, *Cometia* (McLoughlin, 1990a), has a morphology similar to *Rigbya* with fused scales, each bearing a single ovule. The scales of *Cometia* are larger and more leaf-like than those in *Rigbya* and support the separation of these genera (McLoughlin, 1990a). Early Permian deposits in Western Australia have yielded the fructifications *Arberia* (White, 1908) and *Ottokaria* (Zeiller, 1902; Plumstead, 1956b)., The presence of these early glossopterid fructifications supports the hypothesis that glacial retreat was not uniform across Australia (Fielding et al., 2008).

2.4 South American megasporophylls

There is not a wealth of information available for fructifications from South America. The majority of information comes from the Paraná Basin in Brazil and Santa Cruz province in Patagonia, Argentina (White, 1908; Archangelsky and

Bonetti, 1963; Millan, 1969a; Iannuzzi, 2000; Cariglino et al., in press). *Arberia* is a genus that is distinctive from other glossopterid material in having a branching structure with each branch terminating in a shallow cupule containing a single ovule (White, 1908). *Arberia* was first described from Early Permian rocks from Brazil but has since been found across Gondwana (Rigby, 1972; Appert, 1977; McLoughlin, 1995; Adendorff, 2005). *Plumsteadiella*, an Early Permian genus, is a scale leaf or cluster of scale leaves attached to a branch and has been found in both South Africa and Brazil (le Roux, 1966; Millan, 1969a). Additional work needs to be carried out on this genus as the original descriptions liken the morphology to an angiosperm flower and relate the genus to the Bennettitales (Millan, 1969a). *Dolianitia*, also from Brazil, is a branching axis with each branch terminating in a single ovule and would probably fit into the larger genus *Arberia* (Millan, 1967). Late Permian sites in Argentina have revealed the presence of *Plumsteadia* and *Dictyopteridium* but no genera unique to South America (Archangelsky and Bonetti, 1963; Archangelsky, 1992; Cariglino et al., in press).

3. Interpretation Problems

Glossopteris was considered to be a fern by early paleobotanists as no fertile material was known for the group. The earliest reproductive structures assignable to the glossopterids supported a pteridophyte affinity based on the presence of what appeared to be sori on the surface of a leaf. The belief that glossopterids were pteridophytes was so entrenched in the paleobotanical world that material that supported a pteridosperm association of the glossopterids was regarded as

inconclusive and confusing (e.g., *Eretmonia* du Toit, 1932). Not until 1952, 71 years after the first description of glossopterid reproductive material, was conclusive evidence presented that the glossopterids were pteridosperms and not pteridophytes (Plumstead, 1952). Impression specimens showed a sporophyll containing ovules attached to a *Glossopteris*-type leaf. With knowledge of identifying features of glossopterid ovulate structures, specimens were soon found on all other Gondwanan continents and misinterpreted material was provided with accurate descriptions (e.g., *Dictyopteridium* Chandra and Surange, 1976; *Ottokaria* Pant and Nautiyal, 1984).

3.1 Bivalved sporophylls

Unfortunately, the interpretation of the nature of glossopterid reproductive organs provided by Plumstead was incorrect and led to misinterpretations of many described genera (Plumstead, 1956a, 1958b). The part and counterpart examined by Plumstead were interpreted as two separate structures creating a cupulate-like structure (Figs. 9, 10). One half of the cupule is reproductive and contains ovules, the other half is sterile and apparently provides protection for developing ovules. Plumstead suggested that the structure was bisporangiate with one half of the cupule bearing ovules and the other half stamens or microsporangiate structures. This bivalved interpretation (without the bisporangiate interpretation) was applied to much of the described material from Africa and India (e.g., Surange and Chandra, 1972a; Banerjee, 1973; Chandra and Surange, 1977). Although recent studies on South African material have clarified these misinterpretations (Adendorff et al., 2002, Adendorff, 2005; Prevec et al., 2008), most of the Indian material remains incorrectly

diagnosed. In actuality part and counterpart represent the same sporophyll. As is common in splitting a rock to reveal an impression, the surface of the plant is seen on both rock faces. Material that has been inaccurately described needs to be reexamined to provide accurate diagnoses.

It was not until McLoughlin (1990b) presented a new interpretation that more accurate reconstructions of impression material were generated (Figs. 11, 13-14). Instead of impressions, many specimens represent molds or casts of the sporophyll. Ovules were most often no longer attached to the sporophyll at time of deposition. McLoughlin (1990b) presented a reconstruction in which the 'ovules' are the point of attachment of now-dispersed ovules. When the rock is split revealing the plant material, a surface with projections or so-called tubercles (fertile surface) and a surface showing venation (sterile surface) are revealed. Adendorff expanded McLoughlin's interpretation for South African material to clarify fertile surfaces that may not have pronounced tubercles (Figs. 12-14; Prevec et al., 2008). One of the drawbacks of these interpretations is the terminology used to describe the part and counterpart. This problem is addressed in Chapter 2. The once reconstructed bivalved sporophyll with a sterile protective bract over a fertile half actually represents two parts of the same structure. The protective bract is actually the sterile surface of the sporophyll while the fertile bract is the fertile surface of the same sporophyll (Figs. 13-14).

3.2 Sporophyll development

The development of megasporophylls presented by Plumstead (1956a) has also been shown to be incorrect (McLoughlin, 1990b; Prevec et al., 2008). During the pollination stage the two halves of the bivalved structure, the ovulate and sterile/staminate, were separate in order to allow for cross pollination (Fig. 9; Plumstead, 1956a). Once fertilization occurred, the two halves fused together to protect developing ovules (Fig.10). Since the two halves are known to represent a single leaf-like structure, the closing of the two halves to protect the developing ovules is incorrect. It has been suggested that the wings that are present in many of the genera were folded inward to protect developing ovules, and this idea is somewhat supported by evidence from permineralized material (Gould and Delevoryas, 1977; Nishida et al., 2007).

Plumstead also described different appearances on the surface of the fossils (regardless if they were impressions, molds, or casts) as a progression of ovule development on the sporophyll (Figs. 15-17; Plumstead, 1956a). When depressions were present with small tubercles in the center, these were interpreted as ovules at time of fertilization or a sporophyll after the ovules have been shed. Projections were described as swollen sacs that contained developing ovules. The depressions actually represent casts of seed cushions where ovules were attached and sunken into the sporophyll and the central tubercle is the point of ovule attachment (Figs. 15, 17). The projections are not fertilized ovules, but molds of the seed cushions (Fig. 16).

3.3 Optical illusion

Another problem in interpreting fructifications encountered in the present study is an optical illusion that occurs when photographing specimens. The angle of the light on the specimen can change the interpretation of the final image depending on the orientation of the specimen. This problem first came to light when imaging Antarctic impressions of *Plumsteadia* and confusion arose as to whether the image was illustrating projections from the surface or depressions into the rock. When the image was rotated 90°, what once appeared as projections now appeared as depressions (Figs. 18-19). This problem was circumvented in Antarctic specimens by using an extremely low angle of light to dramatically put the surface of the specimen into relief (Chapter 2; Fig. 6). In looking through the literature, this problem has occurred as far back as Plumstead's original publications (Figs. 20-21; Plumstead, 1956a). The orientation of her images at times illustrates the wrong relief on the surface of the specimen (Fig. 20). In turning the page 90°, the correct relief can be seen (Figs. 21-22). With no reference to this optical illusion in any publication on glossopterid fructifications, glossopterid reproductive structures may have been misinterpreted and descriptions, as well as images, misunderstood.

4. Permian of Antarctica

For much of the Permian Antarctica was wholly or partly under ice, although this interpretation has been questioned in recent years, both in Antarctica and in Australia (Fielding et al., 2008; Isbell et al., 2008). As the glaciers retreated, the glossopterids apparently rapidly colonized as evidenced by the presence of *Glossopteris* leaves stratigraphically immediately above glacial tillite (Isbell and

Cúneo, 1996). By the Late Permian, they dominated the landscape, with up to 84% of bedding planes at sites in Southern Victoria Land covered by glossopterid remains (Cúneo et al., 1993). A study on *in situ* trunks reconstructed forest density between 2505 trees/hectare in very young boreal forests, to 263 trees/hectare in more mature forests (Knepprath et al., 2004; Knepprath, 2006). The density of Antarctic forests is comparable to those of extant forests indicating that plant growth was not limited by high latitude conditions, such as temperature and water availability, seen today (Norokorpi et al., 1997). Tree-ring studies on Permian woods from the Antarctica have revealed a unique form of ring structure not seen in present-day woods (Creber and Francis, 1996; Ryberg and Taylor, 2007; Taylor and Ryberg, 2007). The wide rings with a small amount of latewood suggest that plants grew continually through the 24 hours of light present in high-latitude summers. Once the sun reached an angle too low on the horizon for photosynthesis, plants rapidly entered dormancy for the dark winters (Ryberg and Taylor, 2007; Taylor and Ryberg, 2007).

The Late Permian in the Central Transantarctic Mountains has been reconstructed as a foreland basin with a braided river system (Isbell, 1991). Different depositional environments which have been described include backswamp, sandbars, abandoned channels, and lakes based on the presence of mudstones, siltstones, and coarse-to-fine grained sandstones deposited in a low-sinuosity lacustrine environment (Isbell and Cúneo, 1996). Volcanic activity at the head of the foreland basin that formed these deposits generated high levels of volcanic minerals which flowed downstream (Collinson, 1991). The abundant presence of silica from volcanic sands

in the water allowed a rare type of fossilization to occur called permineralization. Plant debris caught in backswamps formed peat bogs, environments in which an anoxic zone forms close to the water's surface when oxygen input into the water is less that the oxygen consumed by aquatic microorganisms, preventing the decay of plant material (Clymo, 1984). These bogs were inundated with silica-rich water which allowed silica permineralization and cellular preservation within the plant organs. The only other place where glossopterid permineralizations are currently known are from Queensland, Australia (Gould and Delevoryas, 1977; Nishida et al., 2004, 2007; Pigg and Nishida, 2006). This rare fossilization process has allowed for some of the most detailed anatomical reports on the glossopterids to come from Antarctic localities. The focus of past studies has been on vegetative parts of the glossopterid plant as these are abundant in the silicified peat and has resulted in anatomical reconstructions of *Glossopteris*, *Vertebraria*, and *Dadoxylon-Araucarioxylon* wood (Schopf, 1965; Maheshwari, 1972; Pigg, 1990; Pigg and Trivett, 1994; Neish et al., 1993; Decombeix et al., 2009).

5. Glossopterid Reproductive Structures from Antarctica

Survey work on the Permian Antarctic landscape has revealed the presence of impression and permineralized megasporangiate structures across the continent, including in the Prince Charles Mountains (White, 1973) , Horlick Mountains (Schopf; 1976), Central Transantarctic Mountains (Cúneo et al., 1993), , and Southern Victoria Land (Kyle, 1974). Only a few genera of ovulate structures are known and none are unique to the continent. The diversity of reproductive structures is also less

than that found on other continents. Most previous work has provided interpretations but few formal descriptions of the fossils (Kyle, 1974; Taylor and Taylor, 1992; Zhao et al., 1995). In this study, reproductive genera of both impression and permineralized fossils from the Transantarctic and Horlick Mountains are described in order to provide details on Antarctic glossopterid morphologies and to compare with those from other Gondwana continents.

Chapter 2

Reproductive diversity of Antarctic glossopterid seed-ferns

1. Introduction

The glossopterids are considered to be pteridosperms, an artificial association of plants based on the production of seeds on a leaf-like megasporophyll. The glossopterids dominated the Gondwana supercontinent (comprising most of modern Africa, Antarctica, Australia, India, New Zealand, and South America) during the Permian, and the most common leaf morphotype, *Glossopteris* (Brongniart, 1828), has been considered an index fossil for the Permian. *Glossopteris* is characterized as a lanceolate leaf with entire margins, a distinctive midrib, which consists of numerous veins, and anastomosing secondary venation. The presence of *Glossopteris* leaves on all Southern Hemisphere continents and India provided some of the first support of the theory of continental drift (Wegener, 1924), as dispersal of a land plant across oceans is rare, suggesting that the continents were in contact with each other during the time of the glossopterids. Another distinctive organ of the glossopterid clade is the root *Vertebraria* (Royle, 1833 ex McCoy, 1847), which is organized into alternating wedges of secondary xylem and air spaces (Neish et al., 1993; Decombeix et al., 2009). The characters that distinguish *Glossopteris* and *Vertebraria*, such as anastomosing venation, entire margined tongue shaped leaves, and alternating wedges of wood and air spaces in roots, are plesiomorphies for the glossopterid clade and thus do not provide a wealth of information on the diversity within the Glossopteridales.

Ovulate and pollen structures assigned to the glossopterids have been found throughout Gondwana. Some genera of ovulate structures, such as *Plumsteadia* (Rigby, 1962), are widespread and can be found throughout the Southern Hemisphere, while others, such as *Denkania* (Surange and Chandra, 1971), are restricted to certain geographical regions. Pollen structures, e.g., *Eretmonia* (du Toit, 1932), *Glossotheca* (Surange and Maheshwari, 1970), and *Squamella* (White, 1978) exhibit a fairly uniform morphology across Gondwana and consist of a small scale leaf bearing pairs of pedicels terminating in clusters of microsporangia. Due to the apparently conservative morphology of the leaves, roots, and pollen organs, the diversity of the group will only be understood by examining the ovulate structures.

The first descriptions of reproductive structures, including *Ottokaria*, *Eretmonia,* and *Dictyopteridium*, were erroneously classified as pollen organs of the Medullosales or as fern sori (Feistmantel, 1881; Zeiller, 1902; du Toit, 1932). Plumstead's identification of glossopterid ovulate structures (Plumstead, 1952, 1956, 1958b) presented the need to revise descriptions of previously described genera (e.g., Zeiller, 1902; du Toit, 1932). Since Plumstead's (1952) first description of glossopterid reproductive structures, more than 30 genera (e.g., Anderson and Anderson, 1985; McLoughlin, 1990a, Adendorff, 2005; Nishida et al., 2007; Prevec et al., 2008) of ovulate structures have been established. Previous work on ovulate structures has generated an abundance of information, but at times confounding results about the true diversity of the group. Descriptions of many genera are abbreviated and do not provide enough information to distinguish between genera.

Extensive work has been carried out on descriptions of reproductive structures from South Africa, India, and Australia (e.g., Surange and Maheshwari, 1970; Pant, 1977; Rigby, 1978; White, 1978, McLoughlin, 1990a, b; Adendorff et al., 2002; Prevec et al., 2008), but there is much less documentation of reproductive structures from Antarctica and South America (e.g., Archangelsky and Bonetti, 1963; Bernardes-de-Oliveira et al., 2000). The lack of information from these continents may be due to the small amount of collected material available for study and has left a large gap in the geographical and stratigraphic distribution of glossopterid reproductive structures.

The Permian was a time of global change and as the glaciers from the late Paleozoic Ice Age retreated, the glossopterid flora migrated into higher latitudes so that by the Late Permian, glossopterids dominated the Antarctic landscape, which was then at near-polar latitudes (Cúneo et al., 1993). The numerous morphotypes of *Glossopteris* provide some indication of the diversity of glossopterids in the landscape, but not a comprehensive view. While the presence of glossopterid reproductive structures has been known from Antarctica for several decades (e.g., Townrow, 1967, Lambrecht et al., 1972, White, 1973, McLoughlin et al., 1997; Rigby et al., 2001), several specimens have not been formally described. Schopf (1976) presented evidence that there were morphological types similar to those found on other continents of Gondwana, but did not describe their unique features. Retallack and Krull (1999) also mention the presence of multiple genera of reproductive organs in Antarctica but did not provide descriptions for any of the specimens. This paper describes impression specimens from various sites in the Transantarctic Mountains,

including Southern Victoria Land and the Beardmore Glacier area, and compares these to species from other Gondwanan continents to provide an indication of the glossopterid diversity in the Late Permian Antarctic landscape.

2. Materials and Methods

Specimens are from the Paleobotanical Collections at the Natural History Museum, University of Kansas and include those collected by W.E. Long and J.M. Schopf during the 1958–1959, 1961–1962, 1963–1964, and 1966–1967 Antarctic field seasons (Long, 1959; Long, 1962, Schopf, 1962, Cridland, 1963), by J. Isbell in the 1985–1986 field season (T.N. Taylor et al., 1989), and by R. Cúneo and T.N. Taylor during the 1990–1991 Antarctic field season. *Plumsteadia* specimens are from Mt. Achernar (84º 22’ 23” S; 164º 37’ 56” E), Beardmore Glacier region, Central Transantarctic Mountains and the Allan Hills (76º 42’ S; 159º 40’ E) in Southern Victoria Land (Fig. 23). *Rigbya, Eretmonia,* and *Arberiella* specimens were collected in the Ohio Range of the Queen Maud Mountains on Mt. Glossopteris (84° 44' S; 113° 43' W; Fig. 23) and Mt. Schopf. (84 48’ 00.0” S; 113 25’ 00.0” W). Impression specimens were imaged with a Leica 5000C digital camera on a dissecting microscope. All measurements were made using ImageJ software (Rasband, 1997–2008). Specimens are housed at the University of Kansas, Natural History Museum, Division of Paleobotany, Lawrence, KS, USA.

2.1 Geological Settings and Age

Mt. Achernar plant fossils were collected approximately 50 meters above a 70 meter thick sill at the top of a north-extending platform in the Upper Buckley

Formation of the Beacon Supergroup (Fig. 24), Beardmore Glacier region (see Taylor et al., 1989 for additional locality information). The Upper Buckley has been dated as Late Permian based on compression fossils and palynomorphs (Farabee et al., 1991) and the Achernar site is considered uppermost Permian (Taylor et al., 1989). The formation consists of sandstones and shales and the plant fossils occur in a dark gray shale (Barrett et al., 1986).

Permian plants from the Allan Hills, Southern Victoria Land, occur within the Weller Coal Measures of the Beacon Supergroup (Fig. 25). The Weller Coal Measures are dated as Lower Permian (Kyle, 1977) based on palynomorphs (Askin, 1995) and overlie glacial deposits of the Metschel Tillite, suggesting that plants rapidly colonized land that was recently exposed by glacial retreat in Victoria Land (Isbell and Cúneo, 1996). The coal measures consist of sandstones, siltstones, shale, and coal. Fossils are found in gray siltstones and mudstones. The sandstones were most likely deposited in paleostreams while the siltstones formed in abandoned channels and were then overlain by mudstones of lacustrine origin (Isbell and Cúneo, 1996).

The Permian rocks on Mt. Glossopteris (84° 44' S; 113° 43' W) and Mt. Schopf (84° 48’ 00.0” S; 113° 25’ 00.0” W) of the Ohio Range, Horlick Mountains, belong to the Mt. Glossopteris Formation (Fig. 26). The Late Permian age of the formation is based on the presence of numerous *Glossopteris* leaves and the presence of the conchostracan *Leaia*, correlated with the Late Permian Lower Beaufort Formation of South Africa (Long, 1964). The Mt. Glossopteris Formation consists of

carbonaceous shales and siltstones that are closely associated with coal beds. All plant fossils are found in a gray shale which may appear tan as the shale becomes weathered. At the interface of the coal and shale, graphite is abundant and, due to high amounts of heat or pressure, only impressions with no cuticular remnants are present (Cridland, 1963).

3. Systematic Paleobotany

Class Glossopteridopsida Banerjee, 1984

Order Glossopteridales Pant, 1982

Family Dictyopteridaceae Maheshwari, 1990 (McLoughlin, 1995)

Genus *Plumsteadia* Rigby, 1962

Type species: *Plumsteadia microsacca* Rigby, 1962

Plumsteadia ovata (Kyle, 1974) emend. Ryberg

Plate 9 Figs. 27-31, Plate 10 Figs. 32-33

Synonymy

1974 *P. ovata* Kyle, p. 720 fig. 1.

1976 Strictoid fertiliger Schopf, p. 42, Plate II figs. 4-5.

1993 *P. ovata* Cúneo et al., p. 33, Plate III fig. 2

1989 *Plumsteadia* sp. Taylor et al., p. 29, figs. 1-2.

Repository: Division of Paleobotany, Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, KS, USA

Locality: Allan Hills (76º 42’ S; 159º 40’ E), Southern Victoria Land, Transantarctic Mountains, Antarctica

Stratigraphic Horizon: Weller Coal Measures; Lower Permian

Emended species diagnosis: Narrowly ovate, multiovulate megasporophyll with acute apex. Megasporophyll has a broad base with medial-basal pedicel attachment. Laminar extension along margin fluted. Ovule cushions flattened, elongate at base of sporophyll; distal cushions spherical and upright. Pits/tubercles in megasporophyll represent position of ovule attachment. Striations on pits/tubercles. Anastomosing venation with scalariform tracheids.

Holotype: VH21 (Department of Geology Paleontological Collection, Victoria University of Wellington)

Type Locality: Mt. Feather, Southern Victoria Land, Antarctica

Type Stratigraphy and Age: Weller Coal Measures; Lower Permian

Description: Megasporophylls measure 14–24 mm in length (mean = 19) and 7–18 mm in width (mean = 11) at the widest point (Fig. 27). The length to width ratio ranges from 1.7–2.0:1. The apex of the specimens is acute. Specimens are either impressions exposed to surface erosion and have no counterpart, or the rock has split along the surface of the sporophyll, providing a part and counterpart. Depressions (part; Fig. 28) in the laminar sporophyll have been previously termed seed cushions and will be referred to as such herein. Projections (counterpart; Fig. 29) in the sporophyll are a cast of the seed cushion and have a small projection in their center called a tubercle. The point of attachment of the ovules (pit or tubercle in previous literature) appears darker than the surrounding matrix (Fig. 30). Ovule cushions near the point of pedicel attachment appear more elongate (Fig. 27). Basal ovule cushions

measure 0.9–1.6 mm long (mean = 1.2) and 0.3–0.7 mm wide (mean = 0.5). More distal, but not part of the wing, ovule cushions measure 0.6–1.4 mm in length (mean = 0.9) and 0.5–0.7 mm in width (mean = 0.6). Cushions on the wing surround the entire sporophyll, measuring 1.3–2.3 mm wide, and are at least 54 in number, with the pit or tubercle at the base of a slightly fluted laminar extension (Fig. 31). This structure has been called a wing in the literature and will be referred to as such in this paper. Striations radiate out from the ovule point of attachment on the seed cushions (Fig. 32). On the part with the vegetative surface, anastomosing veins with scalariform tracheids are seen under SEM (Fig. 33).

Discussion: *Plumsteadia* was first described as *Cistella* (Plumstead, 1958b) but the name was already occupied by a genus of the Orchidaceae (Blume, 1825). Maheshwari (1968) presented the name *Gonophylloides*, while Rigby (1969) provided the name *Plumsteadia* to replace *Cistella*. The genus was created to differentiate between glossopterid megasporophylls with peripheral sterile wings (*Scutum*) and those with a marginal row of ovules on the wing (*Plumsteadia*). The majority of the literature has followed Rigby's classification of *Plumsteadia*, even though *Gonophylloides* has priority. Chandra and Surange (1974a) stated that *Plumsteadia* is a morphogenus and suggested that once enough information is obtained to generate a generic name for specimens, they should then be pulled out of the morphogenus and put into their own taxon and created the genus *Plumsteadiostrobus* based on the description of the sporophyll, ovules and the receptacle. The description of *Plumsteadiostrobus* is inaccurate as glossopterid

reproductive structures are now known not to contain protective sterile bracts. The genus needs to be reevaluated to determine whether there is enough information to follow Chandra and Surange's (1974a) suggestion to generate a new genus once enough information is available to distinguish the specimens from *Plumsteadia.* Classifying specimens into *Gonophylloides* rather than *Plumsteadia* was overlooked until Adendorff (2005) suggested separating *Gonophylloides* from *Plumsteadia* on the basis of megasporophyll length-to-width ratio and the presence of a cordate base. In comparing the Antarctic specimens to those of *Plumsteadia* and Adendorff's interpretation of *Gonophylloides*, the Antarctic material belongs to the genus *Plumsteadia* rather than *Gonophylloides*.

Plumsteadia was originally believed to be a microsporophyll by Rigby (1962), who designated *P. microsacca* as the type species. Further investigations found that rather than being a cluster of pollen sacs, each sac was actually the location of an ovule (Rigby, 1978; McLoughlin, 1990b). Presently there are more than 15 species in this genus and these can be found on all Gondwana continents (Table 2). The unique features of *Plumsteadia ovata*, as presented in this paper, are a narrowly ovate sporophyll with a fluted laminate wing. The image of the holotype provided by Kyle (1974) does not clearly show the pedicel. Kyle described the attachment of the pedicel to the midrib of the sporophyll, but in comparing the orientation of the holotype image to comparable specimens in this study the orientation of the sporophyll to the leaf is inaccurate in Kyle's description. The holotype image shows a cast of seed cushions indicating that the micropylar end of the ovules are facing into

the matrix and towards the associated sporophyll. In other Antarctic specimens of *P. ovata* the pedicel is never seen with the cast of the seed cushions, but with the impression of the seed cushions. This suggests that the pedicel is not observed in the holotype. The *P. ovata*? described by Rigby (1978), and reexamined by this author, cannot be conclusively labeled as *P. ovata* as not enough of the specimen is preserved to determined the shape of the entire sporophyll.

In comparing *P. ovata* with previously described species (Table 2), *P. ovata* most closely resembles *P. jensenii* from the Bowen Basin of eastern Australia (McLoughlin, 1990b). While both are narrowly ovate and have ovules of similar size, *P. jensenii* has smaller overall dimensions than *P. ovata* (Table 2) and *P. ovata* has a fluted margin on the wing while *P. jensenii* has a smooth margin. Specimens of *P. jensenii* have been noted from the Upper Permian of Graphite Peak, central Transantarctic Mountains (Retallack and Krull, 1999), but a re-examination by this author of the specimens cited in that paper shows that they do not conform to the species description, as the specimens are much too broad and do not have the length/width ratio of *P. jensenii* (~1.5:1 vs 2–2.5:1 in the species description [McLoughlin, 1990b]). Antarctica specimens assigned to *P. jensenii* by Retallack and Krull (1999) are fragmentary and assigning them to species is premature. In McLoughlin's (1990b) work on *Plumsteadia* from the Bowen Basin of Australia, he tentatively assigned five fructifications to *Plumsteadia*. In the description and images of these unnamed species (McLoughlin, 1990b Plate 1), *P. ovata* is most similar to *Plumsteadia* sp. A. The dimensions of *P. ovata* and *Plumsteadia* sp. A are the most

similar of all the species in the genus, suggesting that *P. ovata* may have been present in Australia as well as Antarctica.

Family Rigbyaceae Anderson & Anderson, 1985

Genus *Rigbya* Lacey et al., 1975

Type species *Rigbya arberioides* Lacey et al., 1975

Rigbya chtenia Ryberg sp. nov.

Holotype: PM2027, Plate 10, Figs. 34-37

Repository: Division of Paleobotany, Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, KS, USA

Type Locality: Mt. Schopf (84° 47' S; 113° 18' W)

Stratigraphic Horizon: Mt. Glossopteris Formation, Horlick Mountains, Antarctica; Upper Permian

Etymology: Greek: “chteni” – scallop; referring to the scalloped edges of the wing

Species Diagnosis: Petiole terminating in 4–10 laminar structures. Distally the petiole divides up to five times to create dichotomizing pedicels, each terminating in a single laminar structure. Leaf-like cupules constricted basally, expanded and open apically with crenate margins. Parallel striations run from the base of the petiole to the tip of the cupule. Ovules attached at the base of the cupule with tissue surrounding and extending above the micropylar end of the ovule. Ovules small, ovoid with pointed micropylar end.

Description: Laminar structures measure 1.7–4.9 mm in length (mean = 3.2 mm), 0.5–1.9 mm in width (mean = 1.2 mm) at the base and 1.3–5.2 mm (mean = 2.9 mm) at the apex (Fig. 34). The base of the cupules is constricted while the apical portion has a more expanded lamina with scalloped margins (Fig. 35). Each cupule is subtended by unfused pedicels, measuring 1–10.8 mm in length (mean = 3.3 mm), pedicels are formed by close dichotomies from the petiole (Fig. 36). Petioles are 4.3–10.8 mm in length (mean = 6.2 mm). Since petiole attachment to the parent plant was not observed in any specimens, the true length of the petiole is unknown. Striations run from the base of the petiole through the pedicels to the distal end of the cupules. The striations may represent vascular tissue, but definitive xylem tracheids were not present. Only one ovule was observed in attachment in any of the cupules, but swelling in the basal portion or the presence of seed scars in the majority of the cupules indicates that seeds were attached to the cupules (Fig. 37). In one specimen (PM2027), two ovules were observed associated with *Rigbya chtenia*. These measure 1.4–1.5 mm in length and 0.6–1.1 mm in diameter. One ovule is not attached to the lamina of the structure but its orientation suggests that it originated in a nearby cupule (Fig. 34). The second ovule is broadly attached at the base of the cupule indicating that ovules were attached basally in the cupules and surrounded by laminar tissue. Similar morphology between the two ovules suggests that the dispersed ovule is from *R. chtenia*.

Discussion: *Rigbya* was first described from the Upper Permian Normandien Formation in the Mooi District of the KwaZulu/Natal Province of South Africa as a

terminal aggregation of cupules or scale leaves in a flabellate arrangement on a slender stalk (Lacey et al., 1975). The morphology of the structure is unlike many of the other reproductive structures of the glossopterids, but the presence of numerous *Glossopteris* leaves in the same matrix led to a correlation of *Rigbya* with the glossopterids (Anderson and Anderson, 1985). Images of Antarctic *Rigbya* specimens provided by Schopf (1976) were not included in this analysis, as the location of the specimens is unknown. Two species of *Rigbya* have been described to date; *R. arberioides* dominates both South Africa and Australia, while *R. ranunculoides* is found in eastern Australia (McLoughlin, 1995). A distinguishing feature of *Rigby chtenia* sp. nov. is that the apex of the cupules is wider and more crenate than the other two species (Table 3). The pedicels of *R. ranunculoides* are fused from the top of the petiole to the base of the cupules, whereas in *R. arberioides* and *R. chtenia* pedicels are free. Laminar tissue occurs between the stalks at their base in *Rigbya arberioides* but is not seen in *R. chtenia*. Another distinguishing feature of *R. chtenia* is the presence of numerous lobes or fluting of laminar tissue at the apex of the cupule/scale, as opposed to only two lobes of laminar tissue at the apex of the scale in *R. arberioides*. Adendorff (2005) has reexamined South African specimens of *Rigbya arberioides* and suggests that the terminal portion of the reproductive structure is not a cupule enclosing an ovule but a scale with an ovule attached at its base. This may also be the case in *R. chtenia* as in some specimens the cupules appear to be scales (Fig. 37). *Rigbya arberioides* has winged seeds, but no seeds have been described associated with *R. ranunculoides*, and *R. chtenia* ovules appear to have no apparent

wings. The true affinities of *Rigbya* remain unclear, as no specimens have been found attached to a parent plant and there is little information to determine the diversity of this genus across Gondwana.

Family Eretmoniaceae Banerjee, 1984, emend. Maheshwari, 1990

Eretmonia du Toit, 1932, emend. Surange & Maheshwari, 1970

Type species *Eretmonia natalensis* du Toit, 1932

Eretmonia singulia Ryberg sp. nov.

Holotype: PM2046 a, b Plate 11 Figs. 38-40

Repository: Division of Paleobotany, Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, KS, USA

Type Locality: Mt. Glossopteris (84° 44' S; 113° 43' W)

Stratigraphic Horizon: Mt. Glossopteris Formation, Horlick Mountains, Antarctica; Upper Permian

Etymology: Latin: "singuli" – single; in reference to a single terminal sporangium

Species Diagnosis: Microsporophyll with broad petiole expanding into laminar structure with a cuspidate apex. Faint parallel venation with rare anastomoses run the length of the lamina. Two pedicels emerge at apex of petiole; each bears a cluster of sporangia. Pedicels are elongate and dichotomize several times; ultimate dichotomies each terminate in a single sporangium. Sporangia bean shaped, blunt at the proximal end; distal end more bulbous. Each sporangium with longitudinal, anastomosing striations over entire length.

Description: A single specimen was available, consisting of a laminar microsporophyll measuring 15.7 mm in length and 11.8 mm at its widest point (Fig. 38). Additional specimens were imaged by Schopf (1976), and although his images support the species description, the specimens are currently lost, so information from the figured specimens is not included. The apical portion of the sporophyll is broad and comes to a point within a short distance. The petiole is unattached and associated vegetative organs are unknown. Venation in the sporophyll is faint and appears parallel. At the point where the petiole expands into the laminar sporophyll, two pedicels diverge on either side of the petiole. The pedicels dichotomize repeatedly, and each axis terminates in a single sporangium (Fig. 39). Below the first dichotomy, pedicels measure at least 3.3 mm long and 0.3 mm wide. The dichotomizing pedicels create a cluster of more than 30 sporangia. Sporangia are bean shaped and measure 0.9–1.3 mm in length (mean = 1.2 mm), 0.2–0.3 mm in width (mean = 0.2 mm) at the base, and 0.4–0.7 mm (mean = 0.6 mm) at the apex (Fig. 40). Longitudinal, anastomosing, parallel striations are present on the surface of each sporangium and extend from the base to the apex.

Discussion: *Eretmonia* was first described by du Toit (1932) from the Upper Permian Beaufort Group in the KwaZulu/Natal Province of South Africa. Additional species have been described from India and Australia, but the majority of *Eretmonia* specimens are classified under the type species, *E. natalensis* (du Toit, 1932). The initial description of *E. natalensis* was of microsporangia in spoon-shaped depressions on the sporophyll, which were compared to fern sori and thus supported

an affinity with pteridophytes (du Toit, 1932). Only after ovules were found attached to *Glossopteris* scale leaves, indicating affinities with seed plants, were these structures reinterpreted as microsporangiate structures. *Eretmonia* is now described as a microsporangiate structure consisting of a scale leaf with two clusters of sporangia attached to stalks at the apex of the petiole. A few species of *Eretmonia* from India and Australia have been described based on features of the scale leaf–microsporophyll without reference to sporangial attachment, which has resulted in limiting distinctive features of species to the shape of the vegetative scale leaf rather than the reproductive portion of the structure (e.g., Chandra and Surange, 1974b; Rigby et al., 1988). In *Eretmonia singulia* the final dichotomy ended in a single sporangium in contrast to some species described from India (*E. utkalensis, E. hinjridaensis, E. karanpurensis*, Surange & Chandra, 1972a) and Australia (*E. cooyalensis*, Holmes, 1974) in which the final dichotomy contains a terminal whorl of sporangia (Table 4). *Eretmonia singulia* is most comparable to *E. ovata* (Surange and Chandra, 1972a) from India, which contains an acute, triangular apex and dichotomizing pedicels that each terminate in a single sporangium. *Eretmonia singulia* is shorter than *E. ovata* (1.6 cm vs. 2.5 cm) and the apex of *E. ovata* is not as acute as that of *E. singulia*. No detailed description of the sporangia of *E. ovata* is available to compare with this Antarctic species. Since only a few specimens are available for both *E. singulia* and *E. ovata*, they may be morphological variants of the same species, but without more detailed information, linking the Antarctic and Indian specimens is premature.

Family Eretmoniaceae Maheshwari, 1990

Arberiella Pant & Nautiyal, 1960

Type species *Arberiella africana* Pant & Nautiyal, 1960

Arberiella inflectada Ryberg sp. nov.

Holotype: PM2181 a, b Plate 11 Figs. 41-42

Repository: Division of Paleobotany, Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, KS, USA

Type Locality: Moraine Ridge, Mt. Schopf (84° 47' S; 113° 18' W)

Stratigraphic Horizon: Mt. Glossopteris Formation, Horlick Mountains, Antarctica; Upper Permian

Etymology: Latin: "inflectum" – curve; referring to the recurved base of the sporangia

Species diagnosis: Clusters of numerous pollen sacs. Dichotomizing stalks attach to a single sporangium. Sporangia elongate with a bulbous apex and blunt, recurved base. Longitudinal, anastomosing striations present on every sporangium from base to apex.

Description: Individual sporangia are bean shaped and measure 1–2 mm in length (mean = 1.1 mm), 0.4–0.7 mm in width (mean = 0.6 mm) at the apex, and 0.3–0.5 mm in width (mean = 0.4 mm) at the base (Fig. 41). The apex of a sporangium is bulbous while the base is recurved and terminates in a blunt point (Fig. 42). Longitudinal, anastomosing striations run the length of each sporangium (Fig. 42). Associated stalks measure 0.4 mm in width at the widest point and 0.07 mm at the

narrowest point; the length is unknown as pedicel attachment is not observed. One stalk was observed attached to the base of a single sporangium. In one specimen (PM2056) a larger stalk, possibly a pedicel, is present and measures 1.3 mm in length but is not attached to either terminal stalks or a sporophyll. Attachment to the parent plant is unknown and only the presence of stalks and a potential pedicel indicate that the sporangia are attached to each other.

Discussion: *Arberiella* was first described from a Permian deposit in New South Wales, Australia (Arber, 1905). The genus was formally named from material collected from the Late Permian Raniganj Basin of West Bengal, India and homologized with the original Australian material as isolated or groups of sporangia with longitudinal dehiscence (Pant and Nautiyal, 1960). Though *Arberiella* is known from all Gondwanan continents, it is often only classified to genus. Three species of *Arberiella* are known and have been distinguished from each other based on the size of the spores contained within the sporangia. Since size can differ within a species, the attachment of the stalk to the sporangium could be a defining feature of *Arberiella* species, especially if pollen is not available for analysis. *Arberiella africana* has a short truncated base with, while *A. vulgaris* has a base elongated into a narrow neck (Pant and Nautiyal, 1960; Lindström et al., 1997). There is no description of the shape of the sporangia in *A. thomasii* and the images do not allow for an interpretation (Pant and Bhatnagar, 1973). The recurved base (Fig. 42) of *A. inflectada* is a unique feature (apomorphy) for this species. Unfortunately, descriptions of species of *Arberiella* are not common, as most studies have concentrated on the pollen within the sporangia

rather than the structures themselves. The bisaccate-striate pollen morphology has been used to propose a glossopterid affinity in both a stratigraphic and geographic context (e.g., Osborn and Taylor, 1994; Zavada, 1991; Lindström et al., 1997). The lack of species information on *Arberiella* does not help to clarify the diversity of the glossopterids, since there are few characters available to distinguish one type from another.

4. Discussion

4.1 Other Antarctic Genera

Other researchers have noted the presence of several different glossopterid reproductive structures illustrating the diversity of the glosospterids in the Permian of Antarctica. In reviewing these specimens, a number of questions remain, many no doubt due to the generally poor preservation. Retallack and Krull (1999) illustrated *Senotheca kingii* (McLoughlin, 1990a) from the Late Permian of Mt. Crean in Southern Victoria Land, but in examining the specimen (F35124b, Condon Museum, University of Oregon), there is no clear definition of ovules attached on either side of the midvein, which would indicate that this specimen is *Senotheca* rather than a vegetative leaf. Retallack et al. (2005) mention the presence of *Plumsteadia*, *Dictyopteridium*, *Ottokaria*, and *Cometia* from the Permian of the Allan Hills, Southern Victoria Land, and from Graphite Peak in the Central Transantarctic Mountains. After viewing these specimens, *Plumsteadia*, *Dictyopteridium*, and *Cometia* are definitely present in the matrix, but the preservation of *Ottokaria* is very poor and does not definitively establish the presence of the genus in Antarctica.

4.2 Megasporophyll preservation

Experimental studies have shown that impression specimens can split along different sections of the plant accounting for some of the morphological differences seen among specimens of the same species (Rex, 1986; Chaloner, 1999). Antarctic specimens split along the point of ovule attachment, resulting in one half of the fossil (the megasporophyll half) containing depressions (molds) in the location of the seed cushions. In the center of each depression is a pit denoting the position of ovule attachment (Figs. 28, 43c). The counterpart consists of projections (casts) in the location of the seed cushions. In the center of each projection is a circular area which appears as a tubercle and represents the location of ovule attachment (Figs. 29, 43c). Studies on South African material have gone into detail on how glossopterid specimens are presented in both part and counterpart (Adendorff, 2005 text fig. 3.1.2; Prevec et al., 2008 fig. 5) throughout Gondwana. The terminology presented is slightly confusing as the so-called sterile surface does not represent the exterior of the sporophyll, i.e., the surface where no ovules are attached. The "sterile" surface is either the surface with uninterrupted vasculature throughout the sporophyll (Fig. 44), or the surface with pits where the ovules were sunken into the sporophyll (Figs. 28, 46). The so-called fertile surface is either a mold (depressions; Fig. 45) or a cast (projections; Figs. 29, 47) of the ovule cushions. In some cases both the part and counterpart represent fertile surfaces, questioning the use of the term "sterile." Perhaps a more detailed terminology is needed to accurately describe what each specimen represents. Instead of "sterile" surface, better terms botanically would be

sporophyll impression and sporophyll mold (Fig. 43b). The "fertile" surface would then be termed the sporophyll cast (Fig. 43c). While both types of "sterile" surfaces are seen in South African specimens (Figs. 43b, c, 44, 46), only the cast and mold type of preservation are seen in Antarctic specimens (Figs. 28, 29, 43c). Schopf (1976) mentions that Antarctic material has been altered due to volcanism during the Jurassic while South African material has been altered by groundwater leaching and iron oxide deposition. The different taphonomic and diagenetic activities that these fossils may have undergone may explain the differences in preservation.

5. Conclusions

The formal description of four species of glossopterid reproductive organs from Antarctica and their comparison to other Gondwanan species provide the first extensive evidence of the diversity of high-latitude, glossopterid reproductive structures in the Permian. The presence of conservative vegetative organs, including *Glossopteris* leaves and *Vertebraria* roots, indicate the dominance of the glossopterids in Antarctica, but not the true diversity of the landscape. At the present time, there appears to be no genera of reproductive structures unique to Antarctica, suggesting that the flora may have had a connection to floras on nearby continents. Antarctica has been reconstructed as centrally located in Gondwana, and in physical attachment to all other Gondwanan continents in the Late Permian (Stampfli and Borel, 2002). The presence of the Antarctic genera presented here on other Gondwanan continents may indicate that genera expanded their range through Antarctica to other continents. The poorly preserved Antarctic impression specimens

do not reveal enough morphological or anatomical details to determine how unique structures may be to the continent, but the descriptions of these reproductive structures refines the geologic and geographic ranges of these taxa. Further work on Antarctic reproductive structures from the Late Permian will provide a more refined picture as to the true diversity of the Antarctic landscape and the geographic distribution of the glossopterids.

Chapter 3

Lakkosia kerasata gen. et sp. nov., a permineralized megasporangiate glossopterid structure from the Central Transantarctic Mountains, Antarctica

1. Introduction

The Glossopteridales, an extinct group of seed ferns, dominated the Permian Gondwanan landscape. The group is characterized by strap-shaped leaves (*Glossopteris* Brongniart, 1828), pycnoxylic gymnospermous wood (*Araucarioxylon* Philippe, 1993), and distinctive roots with alternating wedges of wood and air spaces (*Vertebraria* Royle, 1833). The reproductive material, especially the megasporangiate structures, are diverse in morphology and distribution and have been well documented for the past half century (e.g., Plumstead, 1952; Surange and Maheshwari, 1970; McLoughlin, 1990a; Prevec et al., 2008). Megasporangiate structures have been described from all Gondwanan continents and morphologically range from a multiovulate sporophyll to a uniovulate cupulate structure. Detailed information on glossopterid reproductive structures have remained relatively limited, however, as little information can be gathered from the poorly preserved impression material. Most impression specimens have been compressed to a two-dimensional structure allowing only gross morphological details to be determined, such as shape and size.

The existence of permineralized specimens was first mentioned in 1970 from an Upper Permian site near Mt. Augusta (now Skaar Ridge) in the Central Transantarctic Mountains, Antarctica (Schopf, 1970a, 1970b, 1976). This silicified chert occurred in the Upper Buckley Formation coal measures and provided evidence of both megasporangiate and microsporangiate structures. Gould and Delevoryas (1977) presented permineralized glossopterids from the Upper Permian Blackwater Group of the Bowen Basin of Australia and gave detailed descriptions of various pollen- and ovule-bearing structures found in the matrix. None of these three authors, however, presented formal descriptions of the reproductive material. The first formal description of any of the permineralized glossopterid reproductive material was that of *Plectilospermum elliotii*, a large ovule found throughout the permineralized deposits from the Permian of Skaar Ridge (Smoot and Taylor, 1986; Taylor and Taylor, 1987). Taylor and Taylor (1992) later described a megasporophyll bearing small ovules, but unfortunately no formal description or name was provided. Zhao et al. (1995) subsequently described a presumably cupulate ovulate structure from Antarctica.

The Australian fossils were finally described and named by Nishida and colleagues (Nishida et al., 2003, 2004, 2007; Pigg and Nishida, 2006), who provided detailed analyses and a formal description of Gould and Delevoryas' (1977) material. *Homevaleia* (Nishida et al., 2007) is thus the first generic name given to a permineralized glossopterid ovulate structure and consists of a megasporophyll that enfolds numerous ovules, similar to some of the multiovulate impression fossils (e.g.

Dictyopteridium Feistmantel, 1881; *Plumsteadia* Rigby, 1962; *Scutum* Plumstead, 1952). The permineralized material from Antarctica, however, does not conform to the genus *Homevaleia*, indicating that there is some diversity among permineralized multiovulate reproductive structures in the glossopterid clade, as would be expected based on the large number of impression genera that have been established.

None of the currently known megasporangiate permineralized structures has been found attached to *Glossopteris*. The assignment of the reproductive structure from Antarctica to the Glossopteridales is based on the abundance of *Glossopteris* leaves in the matrix, up to 85% of the cover at some outcrops in Antarctica (Cúneo et al., 1993), and the presence of similar anatomy in the megasporophyll and vegetative leaves of *Glossopteris*. The reproductive structures are also associated based on the presence of *Protohaploxypinus* pollen found within the pollen chambers of ovules. This paper presents the first formal description of one permineralized ovule-bearing structure from Antarctica.

2. Materials & Methods

Specimens are from a silicified peat deposit from the Skaar Ridge (formerly Mt. Augusta) locality (84º 49' 15.8" S, 163º 20' 18.9"E) in the Central Transantarctic Mountains, overlooking the Beardmore Glacier (Figs. 48-49). Permian rocks on Skaar Ridge are part of the Upper Buckley Formation (Barrett and Elliot, 1973; Barrett et al., 1986) and the peat has been dated as Late Permian based on palynomorphs (Fig. 50; Farabee et al., 1991). The specimens described here were collected during the 1969–1970 Antarctic field season by J.M. Schopf (Schopf, 1970b) and became part of

the University of Kansas Natural History Museum, Division of Paleobotany Collection in 2007 when Schopf's collection was acquired as an orphan collection from The Ohio State University.

Specimens were prepared using the acetate peel technique (Galtier and Phillips, 1999) using 50% hydrofluoric acid to etch the slabs. Peels were mounted on microscope slides using Eukitt. Digital images were obtained using a Leica 5000C camera on a compound microscope and images were minimally processed using Adobe Photoshop CS3. Specimens and all slides and images prepared from them are housed in the University of Kansas Natural History Museum, Division of Paleobotany collections.

2.1 Geological Setting and Age

The Beardmore Glacier region in the Late Permian has been reconstructed as a meandering braided river system (Isbell, 1991). The Skaar Ridge locality is believed to be an abandoned channel that subsequently became a backswamp. The predominance of the rooting system *Vertebraria* supports the presence of a backswamp environment. The peat material was inundated by silica from volcanic activity at the head of the foreland basin of the Transantarctic Mountains stratigraphic basin (Collinson, 1991), and silicified in a fluvial sandstone, based on the presence of mixed chert-sandstone blocks (Taylor and Taylor, 1987).

3. Systematic Paleobotany

Class Glossopteridopsida Banerjee, 1984

Order Glossopteridales Banerjee, 1984

Genus Lakkosia gen. nov. Ryberg

Type species: *Lakkosia kerasata* sp. nov. Ryberg Plate 15 Figs. 51-55, Plate 16 Figs. 56-60, Plate 17 Figs. 61-64, Plate 18 Figs. 66-71

Synonymy:

1976 cuneate-shaped ovule/seeds Schopf, Plate V, Figs. 3-4

1992 megasporophyll Taylor and Taylor, Figs. 1, 3-5

1995 cupulate glossopterid seeds Zhao et al., Figs. 1-2

2007 multiovulate and cupulate megasporophyll Taylor et al., Figs. 1, 3, 5.

Repository: Holotype, paratypes and slides made thereof are housed at the Division of Paleobotany, University of Kansas Natural History Museum collection, Lawrence, KS, USA.

Type Locality: Skaar Ridge, Beardmore Glacier Region, Central Transantarctic Mountains

Stratigraphic Horizon: Upper Buckley Formation, Beacon Supergroup; Late Permian

Etymology: The generic name *Lakkosia* is derived from the Greek term *lakkos* which means pit or depression, to describe the attachment points of the ovules on the sporophyll. The specific name *kerasata* is derived from the Greek *keras* which means horn, to describe the horn-like appearance of the apex of the ovules in some longitudinal sections.

Generic Diagnosis: Laminar megasporophyll with recurved margins and anastomosing venation. Megasporophyll of isodiametric parenchyma cells with

reticulate thickenings, no palisade parenchyma. Epidermis thin, no distinctive midrib, xylem tracheids with scalariform thickenings. Adaxial surface with numerous depressions, each depression contains a single ovule. Vasculature from megasporophyll terminates in the chalazal end of each ovule. Sclerotesta at micropylar end forms two appressed masses of lignified parenchyma cells. Sarcotesta overarches parenchyma masses, seen as horn-like projections in longitudinal section, and creates an opening above the micropyle. Sarcotesta forms two wings. Nucellus free from integument except at base.

Specific Diagnosis. As for the generic diagnosis

Holotype: 13676 D-bot series δ, Figs 51-53, 59; 63-64; 66, 68, 70.

Paratypes: 13676 E-top series q (Figs. 56, 61), 13676 E-top series r (Figs. 55, 69), 13676 D-bot series β (Figs. 54, 57-58, 62, 67)

Description: Ten specimens of both cross and longitudinal sections were analyzed. The megasporophyll measures 7.2–8.5 mm in width (Fig. 51). The length of the sporophyll could not be determined as only a portion of it was preserved in all specimens. The sporophyll is up to 1.5 mm thick and tapers to only a few cells wide in the recurved margins. The margins of the sporophyll recurve, but there is no evidence that they enclose the ovules contained on the adaxial surface as the margin of the sporophylls is not preserved and remains unknown. The isodiametric mesophyll cells measure 0.1–0.2 mm in diameter and many of them contain reticulate thickenings, suggesting that they represent transfusion tissue (Fig. 52). The epidermis is a single layer thick and the cells measure approximately 0.01 mm in diameter. Poor

preservation prevented identification of cellular detail in the epidermis and no stomata were observed in any of the sections. The vasculature of the sporophyll is represented in cross section by a grouping of poorly preserved xylem cells and a space in the specimen where the phloem was probably located (Fig. 53). Xylem cells measure 0.01 mm in width and contain scalariform thickenings (Fig. 54). There is no pronounced midvein which may indicate that either the sporophyll did not have a midvein or that the specimens represent a more distal portion of the sporophyll where a midvein would no longer be prominent. The position of the xylem and the phloem lacunae indicates that the ovules are attached to the adaxial surface of the sporophyll (Fig. 51). No vegetative leaf is seen in attachment to any specimen and the orientation of the sporophyll to a leaf is unknown.

Depressions on the adaxial surface of the sporophyll are present between vascular bundles where there are fewer layers of parenchyma cells in the mesophyll (Fig. 51). The depressions each contain a single ovule attached to the sporophyll by a short stalk (Fig. 55). Vasculature from the sporophyll enters the stalk and apparently ends in the chalazal end of the ovule as no vascular tissue is seen in the sclerotesta. There is also no indication of a chalazal disc of vascular tissue. In cross sections of the megasporophyll, the ovules are tightly appressed to each other rather than being loosely scattered across the sporophyll (Fig. 56). Thin strips of tissue that appear to enclose individual ovules are seen in both transverse and longitudinal sections of sporophylls (Figs. 57-58). Arrangement of the ovules on the sporophyll is unknown,

but it is interesting to note that, in longitudinal section, no two ovules are attached in the same plane of section (Fig. 51).

Ovules measure 2–3.5 mm in length and 1–3.7 mm at their widest point across the apical pads of tissue and wings (Fig. 59). The sarcotesta measures approximately 0.15 mm thick and extends outward on either side of the ovule to create two thin wings (Fig. 60). The sclerotesta measures about 0.1 mm thick. Due to poor preservation of the sarcotesta and sclerotesta, these layers are usually represented by black content that surrounds nucellar tissue (Fig. 59). In longitudinal sections, the differentiation of the sarcotesta and sclerotesta cannot be observed (Fig. 59), but in cross section the differences can be observed in some sections (Fig. 60). A distinctive feature of the ovule is a large mass of lignified parenchyma cells near the apex (Figs. 56, 59) that forms from the sclerotesta. The cells are aggregated into hemispherical masses that are tightly appressed, except centrally where they form the micropyle (Figs. 56, 59, 61). The sarcotesta extends above and arches over these hemispherical masses of tissue, generating an apparent pollen-capture region above the micropyle (Figs. 59, 62); in longitudinal section, these extensions appear horn-like (Fig. 62). The nucellus is fused to the integument only at the base of the ovule (Fig. 63). The presence of *Protohaploxypinus* pollen in both the region above the parenchyma masses (pollen-capture region) and in the pollen chamber supports assignment of *Lakkosia* to the glossopterid clade (Fig. 64). The sporophylls are considered to belong to *Glossopteris schopfii* leaves based on the presence of phloem lacunae in both and the numerous leaves in the surrounding matrix.

4. Discussion

The only other permineralized glossopterid ovulate structure known is *Homevaleia gouldii* (Nishida et al., 2007) from the Upper Permian Blackwater Group of the Bowen Basin, Australia. Both *Lakkosia* and *Homevaleia* are multiovulate sporophylls with ovules borne on the adaxial surface, based on the anatomy of the vascular bundles. Definitive evidence shows that the sporophyll of *Homevaleia* completely encloses the adaxial ovules (Gould and Delevoryas, 1977; Nishida et al., 2007). Although *Lakkosia* has recurved margins, none of the specimens have the distal edge of the margin preserved, so whether the ovules are completely enclosed or not remains uncertain. A major difference between the two genera is that in *Lakkosia*, each ovule is borne in a surface depression on the sporophyll (Fig. 51), whereas *Homevaleia* ovules are completely enmeshed in a network of cells and are not sunken into the megasporophyll (Nishida et al. 2007, figs. 1d, 5a-d). The meshwork of cells in *Homevaleia* develops from the ovules, while the depressions in *Lakkosia* are part of the sporophyll. The sporophyll of *Lakkosia* is much smaller than *Homevaleia* (7–8 mm vs. 14 mm), but the ovules are larger (2–3.5 mm vs. 1.2-1.3 mm in length in *Homevaleia*). The sporophyll of *Homevaleia* has a keel on the abaxial surface, indicating the presence of a midrib. This is absent in *Lakkosia* suggesting that either *Lakkosia* did not have a distinct midrib or the Antarctic specimens represent the distalmost portion of the sporophyll which may not have had a midrib. The mesophyll in *Homevaleia* is separated into two layers of small cells towards the adaxial surface and larger cells towards the abaxial surface, while there is no differentiation of cell

size seen in well-preserved portions of *Lakkosia* mesophyll. *Lakkosia* ovules are tightly packed on the sporophyll (Fig. 56) as opposed to *Homevaleia* (Nishida et al., 2007, figs. 1c, 3), where there is space between ovules. *Homevaleia* has been compared to *Dictyopteridium*, which has laminar tissue present between ovules (McLoughlin, 1990a; Nishida et al, 2007) whereas the tightly compacted ovules in *Lakkosia* would be more comparable to the impression genera *Scutum* (Plumstead, 1952) or *Plumsteadia* (Rigby, 1962). The ornamentation of the sclerotesta into parenchymatous masses at the micropylar end of the ovules is a distinctive character in *Lakkosia* which is absent in *Homevaleia*. Both permineralized genera contain mature ovules still attached to the sporophyll, as the presence of pollen in the pollen chamber attests, but different developmental stages are observed in *Homevaleia* and not in *Lakkosia*. Nishida et al. (2007) observed that the presence of the network of cells enclosing the ovules was more pronounced around more immature ovules and the network was less noticeable around more mature ovules. There is no indication in *Lakkosia* that different specimens have different developmental stages. Explanations for different developmental stages in the Australian material and not in Antarctic specimens could be that they were preserved at different times of the year or that the small amount of material and poor preservation of *Lakkosia* prevented observing variations in development between specimens.

Several isolated permineralized ovules have been described from the Skaar Ridge permineralized peat locality in Antarctica. *Choanostoma verruculosum* is most similar to the ovules found in *Lakkosia*; it is similar in size (~ 2 mm in length) and

has pads of parenchymatous tissue projecting above the micropyle (Klavins et al., 2001). Differences between *Lakkosia* and *Choanostoma* include the presence of a wing in *Lakkosia* and the lignified parenchyma cells forming the micropyle in *Lakkosia* (Klavins et al., 2001). The sarcotesta in *Choanostoma* forms two hemispheres of tissue above the micropyle while in *Lakkosia* the sarcotesta forms a complete ring of tissue above the micropyle. The seed *Plectilospermum* has two wings like that of *Lakkosia*, but is much larger (4.8 vs. 2 mm in length) with a morphology distinctive from *Lakkosia* (Taylor and Taylor, 1987). Ornamentation at the micropylar end is minimal in *Plectilospermum* as opposed to the elaborated sarcotesta and sclerotesta in *Lakkosia*. The presence of several different morphologies of permineralized ovules in the Antarctic peat suggests that there are megasporophyll morphologies yet to be found and the diversity of the Late Permian landscape in Antarctica cannot be determined solely on the basis of the presence of *Lakkosia*.

In comparing *Lakkosia* to compression/impression specimens of the glossopterids, the genus is most similar to the multiovulate-type morphology (i.e., *Scutum* Plumstead, 1952; *Dictyopteridium* Feistmantel, 1881; *Plumsteadia* Rigby, 1962), which consists of a flattened, leaflike megasporophyll bearing numerous ovules on the surface, with or without a wing. The depressions in which the ovules sit are analogous to the seed cushions seen in some impression genera. In *Lakkosia* the tight aggregation of ovules with the seed cushions abutting each other would suggest a close affinity to *Scutum* or *Plumsteadia* as both genera have a tight aggregation of ovules surrounded by a wing (Plumstead, 1952; Rigby, 1962; Adendorff, 2005).

Wings, commonly seen in impression specimens but never in permineralized specimens, could be analogous to the recurved margins seen in permineralized specimens (Adendorff et al., 2002; Prevec et al., 2008). The margins may have curved over the adaxial surface of the sporophyll to provide protection to developing ovules. Once the ovules were mature enough for pollination, the margins may have unfolded to expose the ovules for pollen capture (Nishida et al., 2007). This process is strongly supported in *Lakkosia* since the small opening at the apex of the ovules and the lack of evidence of a pollination droplet may suggest that exposure to wind pollination was required for pollen capture. Until the physiology of the glossopterids is better known, a correlation between the recurved margins and sterile wings cannot be definitively determined. Numerous impressions of potentially glossopterid seeds have been described from throughout Gondwana (Pant and Nautiyal, 1960; Millan, 1969b; Pant et al., 1985; McLoughlin, 1993) as bi-winged seeds, but are all smaller (1-2.3 mm x 0.9-1.2 mm vs. 2-3.5 mm x 1-3.7 mm in *Lakkosia*) than the ovules of *Lakkosia* and do not suggest an association with *Lakkosia*.

A multiovulate structure was described in detail (Taylor and Taylor, 1992) and has sparked a debate as to the orientation of reproductive structures to the sterile portion of the plant (Pigg and Nishida, 2006). Permineralized specimens from both Antarctica and Australia show the ovules attached to the adaxial surface of the sporophyll based on the orientation of the vascular bundles. Impression specimens, where the associated vegetative leaf is present, often show the ovules facing the vegetative leaf, suggesting that ovules are attached to the abaxial surface (Gould and

Delevoryas, 1977; Retallack and Dilcher, 1981, 1988). There are a few impression specimens that indicate that ovules are attached to the adaxial surface and face away from the associated leaf (Pant, 1977; Rigby, 1978; Pant and Nautiyal, 1984), however, preventing resolution on plant orientation based on impression specimens. No leaf has been found associated with permineralized specimens to prove the orientation of the sporophyll to the leaf. The orientation of the megasporophyll is important to understand pollination and also a potential relationship to angiosperms. The glossopterids have been suggested to have been wind pollinated (Retallack and Dilcher, 1988) but there is no conclusive evidence to support this idea. Taylor and Taylor (1992) suggested that if the glossopterids were wind pollinated, pollen capture would not be easily accomplished if the ovules faced a subtending leaf as they would not be readily exposed to pollen in the wind. In this scenario ovules that face away from a subtending leaf would more likely capture pollen, supporting the anatomical evidence that ovules are attached to the adaxial surface of a leaf. In *Lakkosia* the thin layer of tissue that surround each ovule may have extended beyond the recurved margins of the sporophyll to aid in pollen capture and thus do not definitively provide support for the orientation of ovules to a subtending leaf. Until anatomical attachment of the sporophyll to the vegetative leaf and the associated plant can be determined, the orientation of the sporophyll to the rest of the plant cannot be definitively stated.

Zhao et al. (1995) described what was thought to be a cupulate reproductive structure, distinct from the multiovulate form, from the Antarctic permineralized peat, and suggested that it provided evidence of the diversity of glossopterids in Antarctica

(see also Taylor et al., 2007). The present study reveals that this specimen does not represent a cupulate structure, but a multiovulate structure similar to that described by Taylor and Taylor (1992) and now named *Lakkosia*. The additional specimens described here have too many characteristics in common to indicate that these represent separate genera. In serial sections of the so-called cupulate sporophyll, the base of the sporophyll is present, including the vasculature and attached ovules (Fig. 65). Zhao et al. (1995) did not illustrate the attachment of the sporophyll to the ovules, as the base of the sporophyll was not preserved in their sections (Fig. 65g, h). The anatomy of the ovules in the 'cupulate' sporophyll is the same as those in the multiovulate specimens (compare Figs. 66-67). The thin strips of tissue around the ovules in the 'cupulate' specimen, which were previously interpreted as cupule lobes (Zhao et al., 1995), are present in several of the multiovulate specimens, and perhaps all but poor preservation prevents observing them, and appears to be a distinctive feature of *Lakkosia*. This tissue originates at the rise of the seed cushion on the adaxial surface of the megasporophyll (Fig. 68). In some longitudinal sections, the tissue appears to arch over the apex of the ovule and enclose it (Figs. 58, 69); in others the tissue does not enclose the ovule (Fig. 68). In some cross sections, this tissue also appears to completely surround an ovule suggesting a cupule-like feature (Fig. 57). Other sections do not show the presence of this thin, delicate tissue. If the analyzed material represents the distal portion of a sporophyll, this tissue may represent the recurved margin of the sporophyll. However, this does not explain the complete envelopment of the ovules seen in cross section or the anatomical

attachment of the tissue to the sporophyll. The function of these thin strips of tissue is unknown. They do not appear to be homologous to the meshwork of filaments in *Homevaleia* (Nishida et al., 2007), as those arise from the outer layer of the integument, while the structures in *Lakkosia* appear to be attached to the sporophyll. Perhaps this tissue aids in pollen capture in some way, maybe by guiding the pollen to the micropylar opening as seen in some cupulate Paleozoic seed plants (Taylor, 1982). Pollen is present within the strips of tissue, but outside of the ovules, at the base of the seed cushion in both transverse and longitudinal sections (Figs. 70-71).

The glossopterids have been suggested to be the precursors of the angiosperms based on the presence of ovules and a leaf like sporophyll (Retallack and Dilcher, 1981; Melville, 1983). The key difference between gymnosperms and angiosperms is a unitegumented ovule in gymnosperms and a bitegumented ovule in angiosperms. Melville (1983) suggested that the laminar megasporophyll represented a primitive form of a second integument for the glossopterids. This hypothesis is not strongly supported in multiovulate structures, but the proposed cupulate structures (e.g., *Rigbya* Lacey et al., 1975, *Denkania* Surange and Chandra, 1973) would provide stronger support for an angiosperm affinity as the laminar tissue enclosed a single ovule potentially representing a second integument. In *Lakkosia* the presence of thin strips of tissue surrounding individual ovules may represent a primitive form of a second integument. These thin strips of tissue may be proof of a glossopterid affinity for the angiosperms, but until the true purpose of the enclosing tissue can be

ascertained, I am reluctant to propose a definitive relationship between the Glossopteridales and the angiosperms.

The presence of transfusion tissue (Fig. 52) has not been documented in either of the species of permineralized *Glossopteris* leaves from Antarctica (Pigg, 1990), nor in the megasporophyll and leaves from the Bowen Basin (Nishida et al., 2007). Transfusion tissue is a relatively common feature in some gymnosperms and serves either as an auxiliary transport tissue or for water storage (Worsdell, 1897; Esau, 1953). The presence of transfusion tissue is most often found in leaves with a single vein, e.g., many conifers, and provides water transport to the distal portions of the leaf (Worsdell 1897). It has also been suggested that solutes may be transported this way (Canny, 1993). The anastomosing venation in *Lakkosia* does not fit with the model of transfusion tissue distribution based on modern conifers. There is abundant vasculature throughout the leaf to provide transport, the addition of transfusion tissue suggests that the majority of the tissue in the megasporophyll was used for transporting water and solutes. The large, in proportion to the xylem, phloem lacunae (Fig. 53) may indicate that plenty of photosynthates were present for the developing ovules and do not explain the presence of transfusion tissue. The very high-latitude environment that these plants were believed to be growing in may provide support for the presence of the transfusion tracheids (Taylor et al., 1989). Based on the depositional environment (Cúneo et al., 1993) and the structure of tree rings in the peat (Taylor and Ryberg, 2007), there was an abundance of ground water available. If environmental conditions, such as 24 hours of light during the growing season,

necessitated prolonged opening of stomata, water would have been constantly transported from the roots to the leaves in glossopterid plants, and water-storage tissues would have been extremely important in ensuring that the leaf did not suffer from extreme water loss. With the presence of 24 hours of light, there would be continuous, and perhaps rapid, development of ovules which would require transport of large volumes of photosynthates and water that perhaps the vascular system could not provide on its own.

The mass of lignified parenchyma at the micropylar end of the ovules is another distinctive feature of *Lakkosia* and may suggest a link with other groups of Paleozoic seed plants. The parenchyma forms two hemispheres of tissue that are tightly appressed to one another, with the micropyle located centrally between them. These may represent a postzygotic sealing mechanism in which the parenchyma cells expanded after pollen capture and thus sealed the pollen chamber. A similar sealing mechanism occurs in the Paleozoic Callistophytales and Cordaitales, and Mesozoic members of the Cycadales and Ginkogales (Serbet and Rothwell, 1995). Most of the specimens of *Lakkosia* came from a single slab on an individual peat block and may have originated from a single plant thereby not providing potential morphological differences between individual plants. The similar anatomy of the vasculature in both *Lakkosia* and *Glossopteris schopfii* leaves, in addition to the numerous leaves in the matrix surrounding each sporophyll, suggests that *G. schopfii* and *Lakkosia* may be part of the same plant, as suggested by Taylor and Taylor (1992). With no direct attachment, however, a glossopterid reconstruction based on this isolated

megasporophyll is premature. *Lakkosia* contains traits associated with the Glossopteridales and presents traits similar to Paleozoic and Mesozoic plant groups, suggesting that the glossopterids were a group of plants transitioning from an archaic to a more advanced habit.

5. Conclusions

The description of the megasporophyll *Lakkosia*, with attached ovules, provides additional anatomical detail of the glossopterid seed ferns. With this formal description, previous descriptions have been clarified. The unique morphological features of the megasporangiate structure indicate that this is a distinctive genus from previously described permineralized material from Australia. Thin strips enclosing individual ovules in *Lakkosia* may provide support for the hypothesis that glossopterids are ancestral to angiosperms. The presence of transfusion tissue, and the method of postzygotic sealing of the ovule support a strong relationship with the gymnosperms. Therefore, forming a hypothesis on the relationship of the glossopterids with a particular plant group with the information provided by *Lakkosia* is premature. Our current knowledge of only one permineralized megasporangiate structure hinders our understanding of the diversity of Antarctic glossopterids. The presence of at least five ovule morphologies, both described (*Plectilospermum, Choanostoma,* and *Lakkosia*) and undescribed, however, does provide some indication of the diversity of the landscape. With the amount of material available in the Antarctic peat, it is only a matter of time before more structures will be discovered to provide clues to the complexity of the Antarctic landscape.

Chapter 4

A new species of *Arberiella* with a review of microsporangiate organs of the Glossopteridales

1. Introduction

The Glossopteridales are a group of extinct land plants that dominated the Southern Hemisphere during the Permian period (300–252 Ma). Glossopterid fossils dominate Permian terrestrial deposits to such an extent that Permian floras of Gondwana are also known as *Glossopteris* floras. The group consists of numerous genera representing disarticulated parts of the plant; *Glossopteris* (Brongniart, 1828) leaves, *Vertebraria* (Royle, 1833 ex McCoy, 1847) roots, *Araucarioxylon* (Kraus in Schimper, 1870) wood (but see Philippe [1993] on the usage of this name), and various genera of reproductive organs. Many of the reproductive structures are associated with the glossopterids by their presence in the same matrix rather than by organic attachment (e.g., *Rigbya* Lacey et al. [1975], *Arberia* White [1908], and the majority of megasporangiate structures). *Glossopteris* is a widespread and common morphogenus assigned to this group and provides little information as to the true diversity of the group. Some whole-plant reconstructions have been suggested for the Glossopteridales (e.g., Retallack and Dilcher, 1988; Pigg and Nishida, 2006), but no definitive evidence, either attachment or consistent association, is available for such a reconstruction. Until individual organs within the glossopterids can be found in

organic attachment to each other, the true affinities and diversity of the group cannot be determined.

Early descriptions of the reproductive structures of the glossopterids likened depressions on the surface of the leaf to fern sori (Bunbury, 1861; Feistmantel, 1881). Arber (1905) noticed that sac-like bodies were associated with some scale leaves but was hesitant to suggest that *Glossopteris* was not a fern. Scale leaves are considered to be associated with the *Glossopteris* plant based on the similar tongue-shaped, entire margined leaves with anastomosing venation, although they are smaller than a typical *Glossopteris* leaf. *Glossopteris* was originally believed to be a fern and the discussion provided by Arber (1905) leans heavily toward the glossopterids as ferns. His discussion does, however, put forward the similarity between glossopterid sporangia and the microsporangiate structures of cycads and the potential of the glossopterids being pteridosperms. Without the presence of a megasporangiate structure, the definitive nature of the microsporangiate structure described by Arber could not be confirmed. Plumstead (1952) presented the first evidence that the glossopterids were seed plants with descriptions of some ovulate reproductive structures. The previously described sori on glossopterid leaves were reinterpreted as the points of ovule attachment and the sporangia that Arber (1905) described as the microsporangiate structures of the glossopterids.

Little work has been done on glossopterid permineralized pollen structures, most likely because impression material indicates such a conservative morphology that all pollen organs have been placed in only a few genera. If pollen sacs are found

dispersed in the matrix they are given the name *Arberiella*; if attached to a scale leaf they are placed in *Eretmonia* (du Toit, 1932), *Squamella* (White, 1978), *Glossotheca* (Surange and Maheshwari, 1970), or *Nesowalesia* (Pant, 1977) based on the shape of the scale leaf. It should be noted that although several authors have discussed the genus *Squamella* since its first publication (Melville, 1983; Pigg and Taylor, 1993; Adendorff, 2005), the genus is invalidly published according to the Index Nominum Genericorum (http://botany.si.edu/ing/; 8/10/09). White (1978) indicated that *Squamella* was the microsporangiate structure associated with the ovulate genus *Lidgettonia* and that the two genera were synonymous for the plant bearing *Glossopteris linearis* leaves. These two genera have not been found in anatomical attachment and can not be definitively associated with each other thereby invalidating the name *Squamella*. The specimens of this genus do have a glossopterid affinity and will be included in the discussion of microsporophylls of this group.

The only publications to date that have presented information on permineralized pollen structures are Gould and Delevoryas (1977) from the Bowen Basin of Australia, Schopf (1970) from the Transantarctic Mountains, Antarctica, and Lindström et al. (1997) from the Prince Charles Mountains, East Antarctica. The presence of *Protohaploxypinus* pollen grains in the pollen chamber of ovules and in pollen sacs unites the megasporangiate and microsporangiate structures of the Glossopteridales. In the present paper, a new species of *Arberiella* is described from permineralized peat from Antarctica and these specimens are compared with

impression material from across Gondwana to illustrate the conservative nature of the microsporangiate structures of the glossopterids.

2. Materials and Methods

Antarctic specimens are from a silicified peat deposit from the Skaar Ridge locality (84º 49’ 15.8” S, 163º 20’ 18.9”E) in the Central Transantarctic Mountains, overlooking the Beardmore Glacier (Figs. 48-49). The locality on Skaar Ridge is part of the Upper Buckley Formation (Barrett and Elliot, 1973; Barrett et al., 1986) and the peat has been dated as Late Permian based on palynomorphs (Fig. 50; Farabee et al., 1991). Specimens were collected by J.M. Schopf during the 1969–1970 Antarctic field season (Schopf, 1970) and became part of the University of Kansas Natural History Museum, Division of Paleobotany Collection in 2007 when Schopf’s collection was acquired as an orphan collection from The Ohio State University.

Antarctic fossils were sectioned and peeled using the acetate peel technique (Galtier and Phillips, 1999) with 50% hydrofluoric acid and peels were mounted on microscope slides with Eukitt®. Specimens were imaged on a Leica 5000C digital camera using a compound microscope. Images were processed using Adobe Photoshop CS3. Antarctic specimens, slides, and images are housed in the University of Kansas Natural History Museum, Division of Paleobotany collection.

2.1 Geological Setting

The Late Permian Beardmore Glacier region has been reconstructed as a meandering braided river system (Isbell, 1991). The Skaar Ridge deposits are believed to represent a backswamp formed by an abandoned river channel. Volcanic

activity at the head of the foreland basin of the Transantarctic Mountains stratigraphic basin provided a source of silica (Collinson, 1991). The peat is silicified in a fluvial sandstone, based on the presence of mixed chert-sandstone blocks (Taylor and Taylor, 1987).

3. Systematic Paleobotany

Class Glossopteridopsida Banerjee, 1984

Order Glossopteridales Banerjee, 1984

Family Eretmoniaceae Maheshwari, 1990

Arberiella Pant & Nautiyal, 1960

Type species: *Arberiella africana* Pant & Nautiyal, 1960

Arberiella schopfii Ryberg sp. nov. Plate 20 Figs. 72-75; Plate 21 Figs. 76-77

Specific Diagnosis: Aggregations of pollen often surrounded by remnants of the pollen sac walls; exhibits anastomosing longitudinal striations on pollen sac surface. Pollen sac wall consists of one to two layers of rectangular parenchyma cells intermittently separated by a single layer of lignified elongated rectangular cells. Sporangia crescent shaped. Associated stalks contain scalariform tracheid thickenings. Pollen bisaccate, taeniate, of the *Protohaploxypinus* type.

Holotype: 13676 D-bot δ Figs. 72-77

Type Locality: Skaar Ridge

Stratigraphy: Upper Buckley Formation, Beardmore Glacier Region, Central Transantarctic Mountains, Antarctica

Age: Late Permian

Etymology: *schopfii* is in honor of J.M. Schopf who collected the specimens and greatly contributed to Antarctic paleobotany.

Description: Several specimens were available for study in different states of degradation. Most of the specimens were identified by clusters of pollen aggregated into groups (Fig. 72). The external surface of the pollen sacs is identified by longitudinal anastomosing striations that run from the base to the apex of the sporangia (Fig. 73). Numerous *Glossopteris* leaves in the matrix surrounding *Arberiella* provide support for a glossopterid affinity for *A. schopfii* (Fig. 74). Partial sections of the pollen sac wall were preserved, but no complete pollen sac was found. The most complete pollen sacs measure 1.0–2.0 mm in length and approximately 0.2–0.4 mm wide at the base and 0.5–0.8 mm wide at the apex. The sporangial wall is comprised of one to two layers of thin-walled parenchyma cells that measure 16 µm long and 36 µm wide (Fig. 75). Throughout the sporangial wall are sections where there is a single layer of rectangular, possibly lignified parenchyma cells that measure 54 µm long and 29 µm wide and may represent the longitudinal striations on the surface of a sporangium (Fig. 75). Dichotomizing axes that contain tracheids with scalariform thickenings are present throughout the pollen sacs and most likely represent stalks of the sporangia (Fig. 76). Pollen grains have a smooth external surface and endoreticulations of a golden-colored material beneath the saccus surface (Fig. 77). The corpus is globose in shape, contains taeniae (striations) that run across the equator of the grain, and sacci that are attached in a subequatorial position. This pollen appears most similar to the *sporae dispersae* taxon *Protohaploxypinus*.

Discussion: Arber (1905) first described microsporangiate structures from Permian deposits in New South Wales, Australia, but could not conclusively determine that sporangia on the surface of the sporophyll were glossopterid since the group had been defined as a pteridophyte. He compared the specimens to microsporangiate structures of the Cycadales but focused heavily on comparisons to fern groups with the understanding that *Glossopteris* was a fern. No spores or pollen were found in his specimens that would have definitively put the glossopterids into either the pteridophytes or pteridosperms. *Arberiella* was formally described from the Late Permian Raniganj Formation of West Bengal, India as isolated or groups of sporangia with longitudinal dehiscence (Pant and Nautiyal, 1960). *Arberiella* has been found across Gondwana, but studies have focused on the pollen contained within the sporangia rather than on identifying features of the sporangia themselves (e.g. Pant and Bhatnagar, 1973; Zavada, 1991; Lindström et al., 1997).

Only three species of *Arberiella* have been described and these are distinguished by the size of the pollen sacs and the pollen contained within the sacs. Most impression specimens have dehisced and appear as two halves connected at the base of the sporangium. The distinguishing features on impression specimens include the size of the pollen contained within the sacs and the shape of the base of the sporangia. The base in the type species, *Arberiella africana* (Pant and Nautiyal, 1960), is truncated and the expansion of the sporangium occurs close to the base. *Arberiella vulgaris* has a narrow elongate base and *A. thomasii* has no known pollen sac wall, and is known only from clusters of pollen. Comparing the size of the pollen

and sporangia, *A. schopfii* most closely resembles the impression species *A. vulgaris*. Little information is available on details of the sporangial wall of *A. vulgaris* and proposing homologies between the impression material and permineralized material is premature.

A previously described (but unnamed) permineralized *Arberiella* from the Bowen Basin of Australia has a sporangial wall that is a single cell layer and contains bisaccate pollen (Gould and Delevoryas, 1977). The material is not as well preserved as the Skaar Ridge material and can only be identified by clusters of pollen with oblique sections of the exterior surface showing striations (Figs. 78-79). The shape of the sporangia cannot be determined, but the pollen grains within the Australian sporangia are smaller than those from Skaar Ridge (30 x 20 μm vs. 70 x 40 μm) indicating that these are probably two different species of *Arberiella*. Permineralized *Arberiella* from the Prince Charles Mountains in Antarctica has been classified as *Arberiella africana* (Lindström et al., 1997, fig. 1). The sporangial walls are one cell thick and contain the typical surface striations. No transmitted light images of the cells constituting the sac wall are available of the Prince Charles sporangia, but *A. schopfii* sporangia are larger (1–2 x 0.2–0.8 mm vs. 0.7–1.2 x 0.3–0.6 mm), contain two types of cells in the wall, and are up to two cells thick in places, indicating that they are not the same species. The Prince Charles Mountains and the Transantarctic Mountains are on opposite sides of East Antarctica and material from the localities may be more similar to specimens from other Gondwanan continents rather than a pan-Antarctic *Arberiella* species (Fig. 48). Specimens from the Horlick Mountains in

Antarctica contain sporangia that are shorter (830–1600 μm vs 1000–2000 μm) and wider (440–900 μm vs. 200–800 μm) and contain larger pollen (72–100 x 37–42 μm vs. 60–70 x 40 μm) than *A. schopfii*, signifying the presence of at least three species of *Arberiella* in East Antarctica (Fig. 48; Cridland, 1963). The presence of at least three species of *Arberiella* provides some evidence of the diversity of the glossopterid flora in Antarctica in the Late Permian.

4. Discussion

Arberiella sporangia occur with all microsporophyll genera associated with the glossopterids, i.e., *Eretmonia*, *Glossotheca*, *Squamella*, and *Nesowalesia*. The presence of *Arberiella* throughout the Permian with little morphological change suggests that this type of microsporangium evolved early in the life history of the glossopterids. With no definite line of dehiscence observed, the sporangia most likely opened anywhere between the thick cells that constituted the longitudinal striations. The simple parenchyma cells constituting the wall of the pollen sac, the lack of vasculature extending into the sporangia, and the presence of mature pollen indicate that all sporangia are mature and at the point of dehiscence. There is no specialized cell layer, such as an annulus, for dehiscence to occur in a particular portion of the sporangium.

The dichotomizing stalks serve to raise the sporangia above the surface or allow them to hang over the edge of the microsporophyll, thus exposing the pollen to wind currents to be carried to ovules. With no observable nutritive tissue to attract animals, the likelihood of animal involvement in pollination is small. *Arberiella*

sporangia are similar to those seen in extant conifers (e.g. *Picea*, *Sequoia*) that rely on wind pollination; these have thin walls and no definite dehiscence point. Studies on anemophily (wind pollination) in angiosperms have noted that species that rely on this method tend to be located in higher latitudes, are deciduous in nature, produce an abundance of small pollen grains, and have microsporophylls exposed to wind currents (Whitehead, 1969). In the Permian, Antarctica was over the South Pole with much of the land mass of Gondwana above 30° S (Wopfner and Casshyap, 1997), indicating a seasonal climate for much of the continent. The presence of leaf mats (Plumstead, 1958) indicates that *Glossopteris* was a deciduous plant. As in many wind-pollinated angiosperms, the absence of leaves seems to be critical at the time of pollination to ensure that the pollen sacs and the ovules are exposed to the wind. The placement of pollen sacs on the surface of a microsporophyll rather than enclosed in some type of structure also supports an anemophilous habit. In extant plants, thousands of pollen grains are produced in a microsporangia that is wind pollinated, where hundreds of grains are produced in angiosperms that are animal pollinated (Milne et al., 2005). The thousands of pollen grains found in an *Arberiella* microsporangium (e.g., 2656 grains/sporangium, Lindström et al., 2007) support wind pollination. The wide range in size of a *Protohaploxypinus* grain (32 – 176 μm, Lindström et al., 1997) extends beyond the range for wind pollination (20-40 μm) in angiosperms (Whitehead, 1969). However, the presence of sacci in *Protohaploxypinus* add surface area with a minimal increase in mass common in conifer pollen to aid in wind dispersal (Schwendemann et al., 2007). The majority of

the criteria for anemophily are present in the glossopterids supporting a potential for wind pollination. Since no permineralized specimens have been found in attachment to the microsporophyll (scale leaf), it is not possible to determine whether the pollen sacs were anatomically borne on the adaxial or abaxial surface or along the petiole. Microsporangia in gymnosperms can be attached to either surface or around the stalk of the microsporophyll, and thus this character does not help discern how *Arberiella* was attached to the microsporophyll.

For the most part, microsporangiate structures of Paleozoic and Mesozoic pteridosperms consist of branching systems with the sporangia attached to the abaxial surface of a leaf-like microsporophyll (e.g., Lyginopteridales, Callistophytales, Corystospermales) or to terminal branchlets (e.g., Caytoniales) or (Taylor et al., 2009). The genus *Nesowalesia* is similar to the Paleozoic pteridosperms with its cup-shaped sporophyll containing sporangia on the concave surface. *Nesowalesia*, from the Late Permian Illawarra Coal Measures of Australia and Late Permian deposits in Orissa, India, is unlike the other microsporangiate glossopterid structures and is associated with the glossopterids based on the presence of *Arberiella* pollen sacs even though the attachment of the sporangia is unlike that in other glossopterid genera (Pant, 1977). *Nesowalesia* has not been found in attachment to other plant structures and its orientation and organization within the whole plant is unknown. The other three genera of glossopterid microsporophylls are all characterized by a leaf-like sporophyll with pairs of pedicels bearing clusters of sporangia. These include *Eretmonia*, a cosmopolitan genus found throughout Gondwana, *Glossotheca* from

Late Permian deposits in Orissa and Bihar, India (Surange and Maheshwari, 1970), and *Squamella* from the Late Permian Illawarra Coal Measures in New South Wales, Australia (Figs., 80-81). The major difference among these three genera is the number of pairs of pedicels attached to the sporophyll, i.e., one pair in *Eretmonia*, two or more pairs in *Glossotheca*, and an unknown number in *Squamella*. The microsporophyll is often referred to as a scale leaf as it is smaller than a *Glossopteris* leaf and is analogous to fertile scales found in gymnosperms in bearing cluster(s) of sporangia on one side of the scale. Specimens of *Squamella* have scale leaves arranged helically around a central axis forming a pollen cone (White, 1978 figs., 20-21; Melville, 1983). Since scale leaves of *Eretmonia* and *Glossotheca* have never been found attached to the parent plant, they may also have been arranged into cones and the scales may have been dispersed at maturity. If this is the case then the pollen structure of the glossopterids is comparable to pollen structures of other gymnosperms rather than pteridosperms. However, a more recent examination of *Squamella* questions the validity of a cone organization as no fertile material was confirmed attached to the axis and specimens may just represent a branch tip (Pigg and Taylor, 1993).

The Mississippian–Permian Cordaitales have been considered by some authors to be ancestral to the glossopterids (Schopf, 1976). A pollen cone of the cordaites, e.g., *Gothania*, is a compound cone of alternating sterile and fertile scales with pollen sacs borne at the tips of the sporophylls (Daghlian and Taylor, 1979). The glossopterid pollen structures cannot be categorized as simple or compound cones as

the sporophylls are found detached and isolated in the sediments. White (1978) did not indicate whether the scales in *Squamella* were all fertile or if sterile scales were also present. In deposits that contain microsporophylls, numerous scale leaves with no sporangial association are found, which neither supports nor refutes whether glossopterid pollen structures were simple or compound. The large difference between *Gothania* and glossopterid structures is the sporangial attachment. Cordaite sporangia are attached to the tip of the sporophyll while the glossopterids have sporangia attached proximally along the sporophyll. Walchian conifers from the Pennsylvanian show some similarities to glossopterid microsporophylls with a prominent distal lamina that is pointed apically, sporangia that can be either sessile or attached to a stalk, and no definitive area of dehiscence (Mapes and Rothwell, 1998).

As we currently understand them, glossopterid microsporophylls are most similar to those of the Cycadales. The microsporophylls of the extant genus *Cycas* are laminar structures that have microsporangia attached to the abaxial surface; the distal end of the sporophyll is cuspidate to acuminate, similar to the apex of some glossopterid microsporophylls (Hill and Yang, 1999). Several fossil cycads (i.e., *Lasiostrobus*, *Delemaya*, *Androstrobus*) also have microsporophyll morphology that is similar to extant *Cycas* and glossopterids (Taylor, 1970; Klavins et al., 2003; Archangelsky and Villar de Seoane, 2004). The largest difference between cycad microsporophylls and the glossopterid microsporophylls is that the distal end of the cycad sporophyll is turned upward to enclose the developing microsporangia, whereas the glossopterids may have been loosely associated into a cone axis.

Previous studies have suggested the glossopterids as possible ancestors to the angiosperms based on the morphology of the ovulate structures (e.g., Retallack and Dilcher, 1981). In cladistic analyses, most characters for glossopterid microsporangiate structures remain unknown (e.g., Rothwell and Serbet, 1994; Doyle, 2006; Hilton and Bateman, 2006), but with the information provided by in this paper, the mode of dehiscence can now be characterized. No ornamentation or specialized cells in the pollen sac suggest that microsporangia dehisced at a specific point indicating an ectokinetic form of dehiscence. The arrangement of *Squamella* microsporophylls on an axis suggests that the pollen-producing sporophylls of at least one taxon were arranged into a cone-like structure (White, 1978; Melville, 1983). The morphological and anatomical characters of the pollen structures suggest a phylogenetic position closer to gymnosperms rather than angiosperms.

5. Conclusions

The description of *Arberiella schopfii* from the Late Permian of the Transantarctic Mountains provides more detailed information on the morphology of the genus than previous reports. Lignified cells throughout the sporangial walls indicate the position of longitudinal striations observed on the surface of the microsporangia. The simple parenchymatous cells that constitute the walls of pollen sacs suggest that there is no definite zone of dehiscence, but rather opening occurred anywhere between the longitudinal striations. The presence of *Arberiella* on all known taxa of glossopterid microsporophylls and the morphology of permineralized material from Australia and Antarctica supports a conservative morphology of

glossopterid pollen structures across Gondwana. The presence of scale leaves attached in a cone in *Squamella* indicates that microsporophylls in the group may have been attached in a cone-like structure on a terminal shoot, although there are no known specimens of a scale leaf attached in any other manner to a glossopterid plant. The scale leaves and attachment of sporangia on dichotomizing branches suggest a gymnospermous affinity for the Glossopteridales rather than a potential angiosperm relationship.

Chapter 5

Conclusions

The presence of impression and permineralized material from Permian Antarctic deposits provides anatomical information that can be extrapolated to interpret impression fossils of glossopterids on other Gondwanan continents. The numerous taxa of reproductive structures provide evidence for the diversity of the glossopterids at high latitudes. While no genera are endemic to Antarctica, the information they provide may help clarify some discrepancies among related genera on other Southern Hemisphere continents. With erroneous diagnoses for several genera, much work needs to be done to determine the true diversity of the Glossopteridales. This work on Antarctic fossils provides a step forward in clarifying this late Paleozoic group.

Technological advancement in analysis tools presents a unique opportunity to three dimensionally reconstruct individual organs of the glossopterid plant. Amira® software, designed primarily for the medical field, can also be utilized on permineralized structures. The complete ovulate reproductive structure is preserved in the matrix, and making serial peels using the acetate peel technique (Galtier and Phillips, 1999) provides a record of the specimen section by section (Fig. 81). After converting each image to a gray-scale line drawing (Fig. 82) they can be digitally placed one on top of the other to generate a model of the three-dimensional morphology of the entire structure (see figs. 28-36 in Stockey and Rothwell, 2009 for an example). This process was carried out on *Lakkosia* specimens to determine how the structure appeared in life. With no modern analog for the Glossopteridales, being

able to reconstruct the entire organ would be a leap forward in our understanding of glossopterid morphology. Unfortunately, results were less than desirable (Figs. 83-85). The specimens had been so distorted in the peat deposit that changes from section to section were too great to provide a comprehensive model of this megasporophyll. *Homevaleia* material from Australia described by Nishida et al. (2007) is in a much better state of preservation and may provide a cohesive transition from section to section. At this time I do not have enough material to carry out this process on Australian material, but perhaps future work will provide the model needed to reconstruct a multiovulate megasporophyll of the glossopterids.

With more detailed information available on the glossopterids, seed plant phylogenies that have included *Glossopteris* need to be revised (e.g., Rothwell and Serbet, 1994; Doyle, 2006; Hilton and Bateman, 2006). Most authors admit to the diversity of the group, but still score *Glossopteris* as a single terminal. The wide range of megasporangiate structures, from multiovulate to cupulate, suggests that more than one terminal should be included for the glossopterids. Rothwell and Serbet (1994) and Hilton and Bateman (2006) indicate that their phylogenies under-represent the diversity of the glossopterids, and Doyle (1996, 2006) makes no mention of which morphogenera he uses to code the *Glossopteris* plant. Below are characters that need to be revised in these established matrices; character states in bold are those selected by the indicated authors (i.e., R&S = Rothwell and Serbet, 1994; D = Doyle, 2006; H&B = Hilton and Bateman, 2006).

Megasporangiate Characters

34. (H&B) 74. (D): Megasporangium/ovule-bearing structure: 0) pinnate (megasporangia, ovules or 'cupules' in two rows on a dorsiventral structure or pinnate with a three-dimensional fertile position), **1) simple, paddle-like (megasporangia or ovules not in two definite rows)** 2) simple stalk-like, with one megasporangium or ovule, or megasporangia/ovule sessile.

This character state was designed to encompass the multiovulate megasporophylls such as *Scutum*, which is commonly found on all Gondwanan continents. The term paddle-like is never defined and is confusing as it is not a botanical term and can be interpreted to represent numerous different morphologies. My interpretation of this term would be a simple leaf with entire margins, but as to what type of paddle the shape is referencing remains ambiguous. However, with the number of morphologies assigned to the glossopterids, both character states of this trait could be applicable. The pinnate character state (0) could apply to genera such as *Lidgettonia* which has two rows of pedicels attached to a scale leaf. The third character state (2) would apply to the genus *Rigbya* which comprises a group of stalks each terminating in a single ovule. Doyle (2006) envisions the paddle-like megasporophyll as a potential precursor to angiosperm carpel morphology, does not hold up for the glossopterids as they fit into every character state. No resolution as to the position of the glossopterids can be garnered from this character as it now stands.

35. (H&B): Megasporangia/ovules: **0) on lateral appendage or sessile on lateral stem**, 1) terminal on stem, 2) marginal.

The majority of the glossopterid ovulate structures consist of ovules borne on a leaf-like megasporophyll that has been reconstructed as arising either from the midrib or the axil of a subtending vegetative leaf (Pant and Singh, 1974). This character state would support the majority of glossopterid ovulate structures. The relationship of *Rigbya* to the parent plant is unknown and could have been borne in the axil of a leaf or on a branching system similar to that of *Caytonia*. Until anatomical attachment of *Rigbya* can be determined, it cannot be stated with certainly that all glossopterids fall into character state 0 or 1.

38. (H&B) 78. (D): Megasporangium/ovule **(0 H&B, 1D): with no closely enclosing structure**, (0 D, 1 H&B) in radial, lobed 'cupule', 2) in anatropous 'cupule' or outer integument, 3) in orthotropous, unlobed 'cupule' or outer integument, 4) in bipartite outer integument derived from two primordia.

Confusion arises immediately as to what "closely enclosing structures" entail. In the permineralized *Homevaleia* from Australia, for example, the margins of the megasporophyll are rolled inward and partially to completely enclose the developing ovules. The relation of the enclosing structure to the ovules is not specified in the phylogenetic matrices and thus brings into question the chosen character state. Impression material of Glossopteridales does not indicate the presence of enclosing structures, but the majority of these specimens have shed their ovules, so perhaps the

differences result from developmental stages. In addition, *Lakkosia* megasporophylls indicate that, at least in this genus, each individual ovule is enclosed in its own structure. *Lakkosia* would be coded as character state 3, creating a polymorphism for this character. This character traditionally associates the glossopterids with pteridosperms, but now would also bring them closer to the Bennettitales, some conifer groups, and even angiosperms.

52. (H&B) 40. (D) Symmetry of ovuliferous shoot: **0) radial**, 1) bilateral.

No glossopterid megasporophyll has radial symmetry. Some of the megasporophylls were originally interpreted as a radial cone (e.g., Surange and Chandra, 1972b), but more recent studies on *Dictyopteridium* have shown that ovules are contained on only one surface of the sporophyll negating the supposed radial symmetry (McLoughlin, 1990a). Cupulate-like structures do not fit into this character state either. *Lidgettonia* would be considered bilaterally symmetrical, as it has two rows of cupulate-like structures on one surface of the sporophyll. *Rigbya* would also be bilateral as the cupules in this genus are arranged in a fan shape and occur in a single plane.

70. (H&B) 40. (R&S) Integumentary vascularization: 0) not vascularized, 1) vascularized.

This character was classified by Hilton and Bateman (2006) and Rothwell and Serbet (1994) as unknown, since vascularization is generally not seen in impression

fossils. With two permineralized genera now known, integuments are both vascularized (*Homevaleia*) and unvascularized (*Lakkosia*). This character was generated to help distinguish vascularization patterns in Paleozoic ovules. The glossopterids include features common in both Paleozoic and Mesozoic pteridosperms and the ambiguous nature of the ovule vascularization may indicate the transitional nature of the glossopterids from older groups to more derived groups.

71. (H&B) 101. (D) Megasporangium/nucellus vascularization: 0) not vascularized, 1) vascularized.

Hilton and Bateman (2006) scored this character as unknown. As with the last character, the anatomical preservation of ovules has clarified this feature. No vascularization is seen in the nucellar tissue of any permineralized ovules that have been associated with the glossopterids, including *Lakkosia* and *Homevaleia* (Nishida et al., 2007) ovules, or dispersed ovules *Plectilospermum* (Taylor and Taylor, 1987) and *Choanostoma* (Klavins et al., 2001), and the group would therefore be scored as 0) not vascularized.

23. (R&S) Sporangium bearing structures (sporophylls or analogous structures): **0) not aggregated**, 1) aggregated but not modified into strobili with determinate growth, 2) ovulate structures not aggregated, microsporophylls forming simple cone, 3) megasporophylls aggregated but not modified into strobili with determine growth, microsporophylls forming simple cones, 4) forming simple cones,

5) forming compound ovulate cones and simple pollen cones, 6) forming compound cones

The majority of glossopterid reproductive organs occur as isolated and unattached sporophylls. White (1978), however, described the presence of microsporophylls aggregated into a cone structure (*Squamella*). The scale leaf of *Squamella* is similar to other microsporophylls and even some megasporophylls (i.e., *Lidgettonia*), suggesting that simple cones may have been produced in some of the glossopterids. Until anatomical attachment of sporophylls to the parent plant are known, assuming that sporophylls are aggregated or not aggregated is premature. Some morphologies would be classified as not aggregated, but with suggested organization of microsporophylls (White, 1978, Melville, 1983), the more appropriate character state may be that of ovulate structures not aggregated (the arrangement of *Lidgettonia* is unknown) and that microsporophylls form simple cones. This character state groups the glossopterids with the Taxaceae.

30. (R&S) Ovule or homologue: 0) not enclosed, 1) enclosed in one vascularized structure consisting of more or less coalesced processes (telomes), **2) enclosed in one vascularized structure consisting of a more or less rolled or recurved laminar structure**, 3) enclosed in one unvascularized layer of tissue, 4) enclosed in two layers of tissue

With new information provided by *Lakkosia*, we now know that at least one genus of ovulate reproductive structures may have been enclosed by at least two

layers of tissue. The unpreserved margins of *Lakkosia* may be like the recurved laminar structure of *Homevaleia* that encloses developing ovules. The additional structure which encloses individual ovules in *Lakkosia* suggests that either character state 3 or 4 would be a plausible for this taxon. Unfortunately, poor preservation does not solve the question as to whether the tissue enclosing individual ovules was vascularized or not.

Microsporangiate structures

Many of the characters coding for glossopterid microsporangiate structures in previous phylogenies do not need to be revised as the morphology of microsporophylls appears to be fairly conservative across the clade. One character in Doyle (2006) and Hilton and Bateman (2006), previously scored as unknown, can now be scored based on anatomical information from the Antarctic *Arberiella* pollen sacs.

47. (H&B) 53. (D) Microsporangial dehiscence: 0) ecto/endokinetic, 1) endothecial.

The simple structure of the pollen sac wall seen in *Arberiella schopfii* suggests that there was no specialized structure to aid in opening the sporangia, indicating an ectokinetic form of dehiscence. The longitudinal ruptures seen in many impression specimens of *Arberiella* (e.g., Lindström et al., 1997) suggest that the wall broke open along weak points of the pollen sac. This character states unites the glossopterids with both pteridosperms and conifers providing support for a gymnospermous affinity for the group.

With new anatomical information from *Lakkosia* and *A. schopfii*, several characters would now shown polymorphic character states, a clear indication that more than one terminal needs to be generated for the glossopterids. There are at least three distinctive morphologies for megasporangiate structures. The multiovulate megasporophyll is what previous authors have coded for the single glossopterid terminal in phylogenetic matrices. The pedicellate morphology, including such genera as *Lidgettonia* and *Denkania*, would fill a niche not considered in any phylogenetic studies. Interestingly enough, these genera with pedicellate morphology have been illustrated by some authors as potential angiosperm precursors, but not included in a matrix (Retallack and Dilcher, 1981, fig. 4; Doyle, 2006, fig. 2). The third morphology that could be associated with the glossopterids is the pedicellate-cupulate *Rigbya*. This morphology is not taken into any consideration in phylogenies. Its association with the glossopterids is based on cursory evidence, but represents a morphology that was widespread in the Southern Hemisphere at this time and should be represented in seed plant phylogenies once we know more about the plant that bore it.

One of the largest problems that appear to arise out of studying the reproductive structures of the glossopterids is the gymnospermous affinity of microsporangiate structures, and a potential angiospermous affinity for the megasporangiate structures. Most characteristics of the microsporophylls strongly unite the Glossopteridales with gymnosperms. The enrolled megasporophyll seen in permineralized material indicates a possible means of carpel evolution. The

megasporophyll, at least in *Homevaleia*, encloses developing ovules and has a small opening presumably to allow for pollination, similar to Mesozoic seed ferns (e.g., *Caytonia*, *Petriellaea*, Taylor and Taylor, 2009) with known gymnospermous pollination or similar to an angiosperm carpel. The additional enclosing structure in *Lakkosia* may indicate a potential to form a second integument, a key characteristic for angiosperms; however, the structure appears to arise from the sporophyll rather than the ovule as expected in primitive secondary integumentary structures.

In the most recent seed plant phylogenies (e.g., Doyle, 2006; Hilton and Bateman, 2006), *Glossopteris* is sister to *Caytonia* and *Pentoxylon* providing support for an angiosperm ancestry for the glossopterids as all three groups have been suggested as angiosperm precursors (Doyle, 2008). In addition, the morphological characters aligning *Glossopteris* with Mesozoic seed plants indicates that the glossopterids may have been a morphologically transitional group from plants with a morphology adapted to growing in the coal swamp environment of the Carboniferous to a morphology adapted to the drier environments of the Mesozoic. Greater resolution within the Glossopteridales will help determine their position in a seed plant phylogeny as either more derived than conifers and sister to the Gnetales and angiosperms (Doyle, 2006; Hilton and Bateman, 2006) or less derived and sister to all other seed ferns (Rothwell and Serbet, 1994).

A great deal of work still needs to be done on the morphology of glossopterid reproductive structures to understand the diversity of this group that dominated Gondwana for fifty million years. The present study of Antarctic glossopterid fossils

represents the first concerted systematic work on glossopterid reproductive organs from the continent which represented the center of Gondwana during the Permian. With new interpretations on how impression specimens are exposed on the rock face, accurate descriptions of glossopterid material from all Gondwanan continents can be evaluated to determine the three-dimensional morphologies for ovulate structures. Future work on glossopterid reproductive morphology from all Gondwanan continents will create a more cohesive and more universal understanding of the reproductive biology of this group.

Table 1: List of genera of reproductive structures assigned to the Glossopteridales. Genera in bold in last column are the genera to which the original material has been reassigned or proposed for reassignment (Adendorff, 2005, unpublished dissertation). Non-bold genera are those informally assigned to the genus. AQ = Antarctica, ZA = South Africa, AR = Argentina, AU = Australia, IN = India, BR = Brazil

Genus	Authority	Sex	Type Locality	Age	Location	Status
Arberia	White 1908	?	Southern Brazil	Lower Permian	BR, ZA, IN, AU	***Arberia***
Arberiella	Pant & Nautiyal 1960	?	West Bengal, IN	Permian	IN, AU, ZA, AQ	***Arberiella***
Austroglossa	Holmes 1974	?	New South Wales, AU	Upper Permian	AU	***Austroglossa***
Bifariala	Prevec et al. 2008	?	KwaZulu/Natal, ZA	Upper Permian	ZA	***Bifariala***
Cistella	Plumstead 1958	?	KwaZulu/Natal, ZA	Upper Permian	ZA, IN, AU	***Plumsteadia***
Cometia	McLoughlin 1990	?	Queensland, AU	Upper Permian	AU	***Cometia***
Denkania	Surange & Chandra 1973	?	West Bengal, IN	Upper Permian	IN	***Denkania***
Derbyella	White 1908	?	Brazil	Lower Permian	BR	*??*
Dictyopteridium	Feistmantel 1881	?	West Bengal, IN	Permian	ZA, IN, AU	***Dictyopteridium***
Dolianitia	Millan 1967	?	Santa Catarina, BR	Lower Permian	BR	***Arberia***
*Elatra**	Adendorff 2005	?	KwaZulu/Natal, ZA	Upper Permian	ZA	***Elatra****
Eretmonia	du Toit 1932	?	KwaZulu/Natal, ZA	Upper Permian	ZA, AU, IN, AQ	***Eretmonia***
Estcourtia	Anderson & Anderson 1985	?	KwaZulu/Natal, ZA	Upper Permian	ZA	***Estcourtia***
Fetura	Benecke 1976	?	KwaZulu/Natal, ZA	Upper Permian	ZA	***Dictyopteridium***
Gladiopomum	Adendorff et al. 2002	?	KwaZulu/Natal, ZA	Upper Permian	ZA	***Gladiopomum***
Glossotheca	Surange & Maheshwari 1970	?	West Bengal, IN	Upper Permian	IN	***Glossotheca***
Gonophylloides	Plumstead 1958, Maheshwari 1968	?	KwaZulu/Natal, ZA	Upper Permian	ZA	***Gonophylloides***
Hirsutum	Plumstead 1958	?	KwaZulu/Natal, ZA	Upper Permian	ZA	***Bifariala***
Homevaleia	Nishida et al. 2007	?	Queensland, AU	Upper Permian	AU	***Homevaleia***
Isodictyopteridium	Rigby 1972	?	Queensland, AU	Upper Permian	AU	*Dictyopteridium*
Jambadostrobus	Chandra & Surange 1977	?	West Bengal, IN	Upper Permian	IN	*Plumsteadia*
Kendostrobus	Surange & Chandra 1974	?	West Bengal, IN	Upper Permian	IN	no longer glossopterid
Lanceolatus	Plumstead 1952	?	KwaZulu/Natal, ZA	Upper Permian	ZA, IN, AR, AU	***Plumsteadia***
Lidgettonia	Thomas 1958	?	KwaZulu/Natal, ZA	Upper Permian	ZA, AU, IN	***Lidgettonia***
Mooia	Lacey et al. 1975	?	KwaZulu/Natal, ZA	Upper Permian	AU	***Lidgettonia***
Nesowalesia	Pant 1977	?	New South Wales, AU	Permian	AU, IN	***Nesowalesia***
Ottokaria	Zeiller 1902	?	West Bengal, IN	Permian	ZA, IN, AU, BR, AR	***Ottokaria***
Palmotophyllites	Maithy 1965	?	West Bengal, IN	Permian	IN	***Palmotophyllites***

Table 1 cont.

Partha	Surange & Chandra 1973	?	West Bengal, IN	Upper Permian	IN, AU	*Lidgettonia*
Pluma	Plumstead 1958 emend. Maheshwari 1968	?	KwaZulu/Natal, ZA	Upper Permian	ZA	***Scutum, Gladiopomum***
Plumsteadia	Rigby 1963	?	Queensland, AU	Upper Permian	AU, AQ, IN, ZA, BR, AR	***Plumsteadia***
Plumsteadiella	Le Roux 1966	?	KwaZulu/Natal, ZA	Permian	ZA, BR	*Plumsteadiella*
Plumsteadiostrobus	Chandra & Surange 1977	?	West Bengal, IN	Upper Permian	IN	*Plumsteadia*
Rigbya	Lacey et al. 1975	?	KwaZulu/Natal, ZA	Upper Permian	ZA, AU, AQ	***Rigbya***
Rusangea	Lacey et al. 1975	?	KwaZulu/Natal, ZA	Upper Permian	ZA	***Lidgettonia***
Scopus	Benecke 1976	?	KwaZulu/Natal, ZA	Upper Permian	ZA	***Plumsteadia***
Scutum	Plumstead 1952	?	KwaZulu/Natal, ZA	Upper Permian	ZA, IN, AU	***Scutum***
Senotheca	Banerjee 1969	?	West Bengal, IN	Upper Permian	IN, AU	***Senotheca***
Squamella	White 1978	?	Queensland, AU	Upper Permian	AU	***Squamella***
Vannus	Plumstead 1963	?	KwaZulu/Natal, ZA	Upper Permian	ZA	***Vannus***
Venustostrobus	Chandra & Surange 1977	?	West Bengal, IN	Upper Permian	IN	*Scutum*
*Vereenia**	Adendorff 2005	?	KwaZulu/Natal, ZA	Upper Permian	BR, ZA	***Vereenia****

*Not yet validly published.

Table 2: List and comparison of *Plumsteadia* species. All measurements in mm. (SVL = Southern Victoria Land, AQ = Antarctica, AU = Australia, ZA = South Africa, Qld = Queensland, AR = Argentina)

	Previous names	Length	Width	Shape	Apex	Base	Ovule	Locality	Age
Plumsteadia ovata this paper		14-24	8-18	lanceolate	acute	rounded	0.6-1.6 x 0.3-0.7	SVL, AQ	Late Permian
P. ovata Kyle, 1974		40	25	broadly ovate	tapered	broad	1.5 x 1	SVL, AQ	Late Permian
P. jensenii McLoughlin, 1990		12-15	5-7	narrow	?	?	1 long	Qld, AU	Late Permian
Plumsteadia sp. A McLoughlin, 1990		20-24	9-11	elliptical	?	?	1.2 wide	Qld, AU	Late Permian
P. natalensis Lacey et al., 1975		18-28	7-12	ovate-lanceolate	pointed	rounded	?	KwaZulu/Natal ZA	Late Permian
P. sullivanii Rigby et al., 2001		24	8	narrowly obovate	?	?	Marginal: 1.8	Prince Charles Mts. AQ	Permian
P. ampla White, 1963	*Cistella ampla*	35	30	pear-shaped	?	?	2.5-3 x 3-4.3	Qld, AU	Late Permian
P. indica Maheshwari, 1964		21+	11	broadly elliptical			?	West Bengal, INDIA	Late Permian
P. gibbosa Anderson & Anderson, 1985	*Scopus gibbosus; S. confertus; S. didiscus*	6-38	3-14	narrowly ovate, lanceolate	obtuse	oblong truncate	1-1.5 x 0.8-1.1	KwaZulu/Natal ZA	Late Permian
P. bowenensis White, 1963	*Cistella bowenensis*	30	8	lanceolate	rounded	?	1 x 0.6	Qld, AU	Late Permian
P. semnes Rigby, 1978		32-43	12-20	?	bluntly acute	cordate	2.5 x 1.2	Qld, AU	Early Permian
Plumsteadia ? Archangelsky & Bonetti, 1963		35	22	?	?	?	2 x 1	Santa Cruz, AR	Middle-Late Permian
P. lerouxii Adendorff, 2005		26.9-42.3	4-10.5	lanceolate	sharply acute -acuminate	rounded-truncate	0.8-2.4 x 0.6-1.8	Gauteng, ZA	Early Permian
Plumsteadiostrobus ellipticus Chandra & Surange, 1975b		?	?	elliptical	?	?	?	West Bengal, INDIA	Late Permian
P. stricta Plumstead, 1958	*Cistella stricta; Gonophylloides strictum*	23	15	ovate and auricular	?	?	?	Gauteng, ZA	Early Permian
P. waltonii Plumstead, 1958	*Cistella waltonii; Gonophylloides waltonii*	19-20	13-16	pedicellate	?	cordate	1.4-2.7 x 0.9-1.5	Gauteng, ZA	Early Permian
P. microsacca Rigby, 1962		27	9	?	?	?	0.8-1.4 x 0.5-0.7	Qld, AU	Late Permian
P. pedicellata Cariglino et al., 2009		15	7	obovate	retuse	acute	0.5	Santa Cruz, AR	Middle-Late Permian

Table 3: List and comparison of all *Rigbya* species. All measurements in mm. (AQ = Antarctica, NSW = New South Wales, AU = Australia, ZA = South Africa)

	Cupule Length	Cupule Width	Cupule Shape	Apex	# cupules	Petiole Width	Ovule dimensions	Locality	Age
R. chtenia This paper	1.7 - 5	1.3 - 4	elongate, spathulate, laminar	expanded, fluted	up to 10	?	? wings	Horlick Mts., AQ	Late Permian
R. ranunculoides McLoughlin 1995	3 - 5	2 - 3.5	elliptical; lanceolate-obovate spathulate	expanded; blunt	4-6	1	? wings	NSW, AU	Late Permian
R. arberioides Lacey et al. 1975	3 - 3.5	2.5 - 3	elongate-spathulate w/ 2 terminal lobes	?	up to 10	0.5 - 1	winged	KwaZulu/Natal, ZA	Late Permian

Table 4: List and comparison of all *Eretmonia* species. All measurements in mm. (AQ = Antarctica, AU = Australia, NSW = New South Wales, ZA = South Africa)

	Scale-leaf	Terminal sporangia	Sporangium	Locality	Age
E. singulia This paper	Cuspidate apex	dichotomous	1.3 x 0.6	Horlick Mts, AQ	Upper Permian
E. ovata Surange & Chandra 1974 (*E. ovoides* in Rigby et al., 1988)	Ovate; triangular apex	dichotomous	?	West Bengal, INDIA	Upper Permian
E. utkalensis Surange & Maheshwari 1970	Broad base; acute apex, dichotomous venation	6-8 in a terminal whorl	1.2-1.5 x 0.5-0.8	West Bengal, INDIA	Upper Permian
E. hinjridaensis Surange & Maheshwari 1970	Spathulate, apex broadly rounded	? terminal arrangement	1.3-1.5 x 0.6-0.7	West Bengal, INDIA	Upper Permian
E. karanpurensis Surange & Maheshwari 1970	Expanded orbicular	6-8 in a terminal whorl	1.4-1.6 x 0.5-0.75	Bihar, INIDA	Middle Permian
E. balmei Rigby et al. 1988	More elongate & apically acute than others	?	?	Western Australia, AU	Early Permian
E. emarginata Chandra & Surange 1975a	Lanceolate, 2-4 midveins, apex long & acute	?	?	West Bengal, INDIA	Upper Permian
E. cooyalensis Holmes 1974	Orbicular-roundly triangular	12 in a whorl	2.5 x 1.5	NSW, AU	Upper Permian
E. natalensis du Toit 1932	Pedicellate; bluntly rounded apex	?	1-2 x ?	KwaZulu/Natal, ZA	Upper Permian

Plate 1 Figs. 1-3 *Glossopteris* leaves. Fig. 1: Impression of typical *Glossopteris* sp. leaf with distinctive midrib and anastomosing venation. University of Western Australia collection, no catalog number. scale bar = 1 cm. Fig. 2: Impression of *Glossopteris* sp. leaf showing attachment of leaves in a whorl. Australian Museum #AMF85070. scale bar = 2 cm. Fig. 3: Impression of whorl of *Glossopteris* sp. leaves compressed vertically. Australian Museum #AMF78254. scale bar = 2 cm.

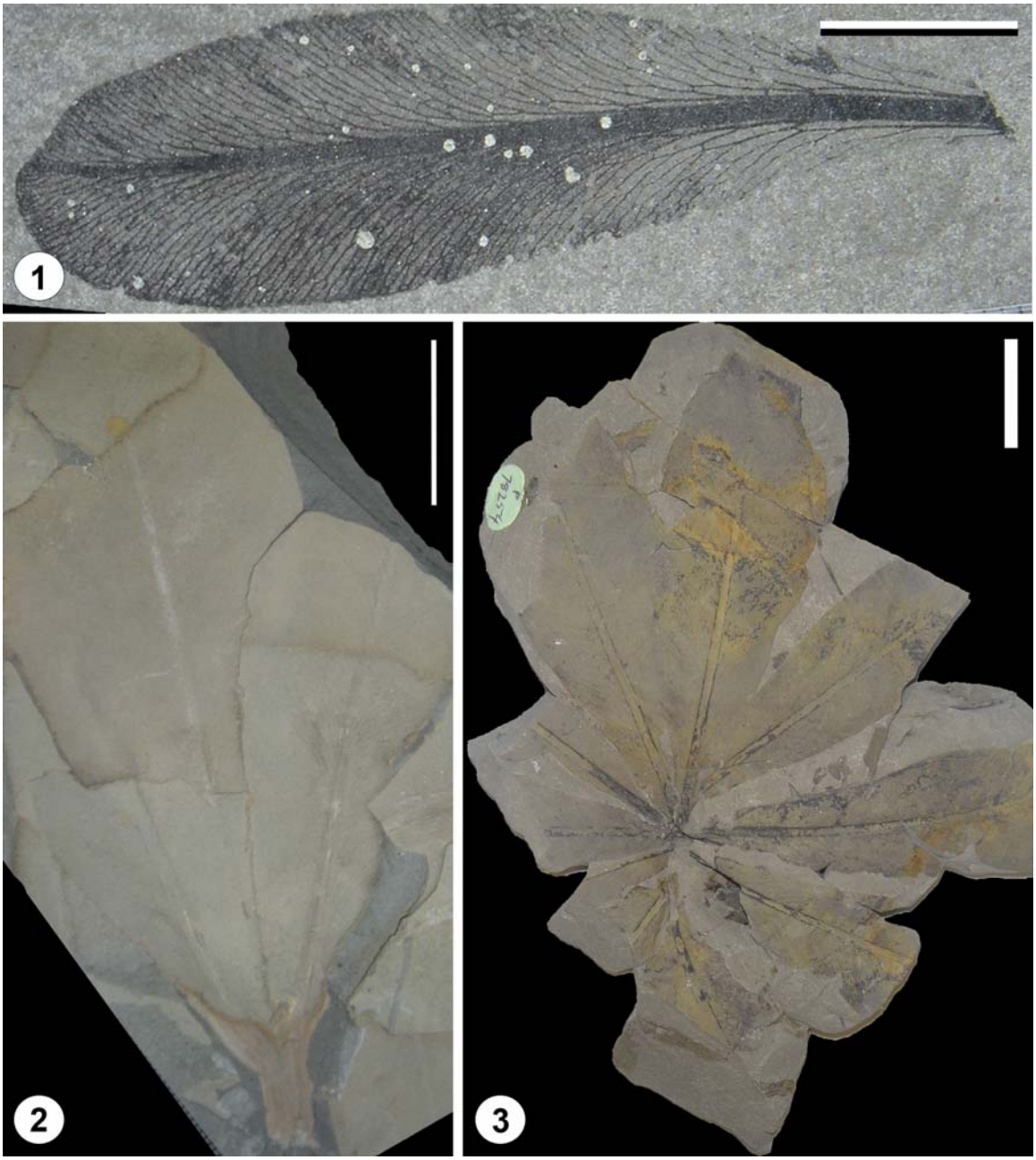
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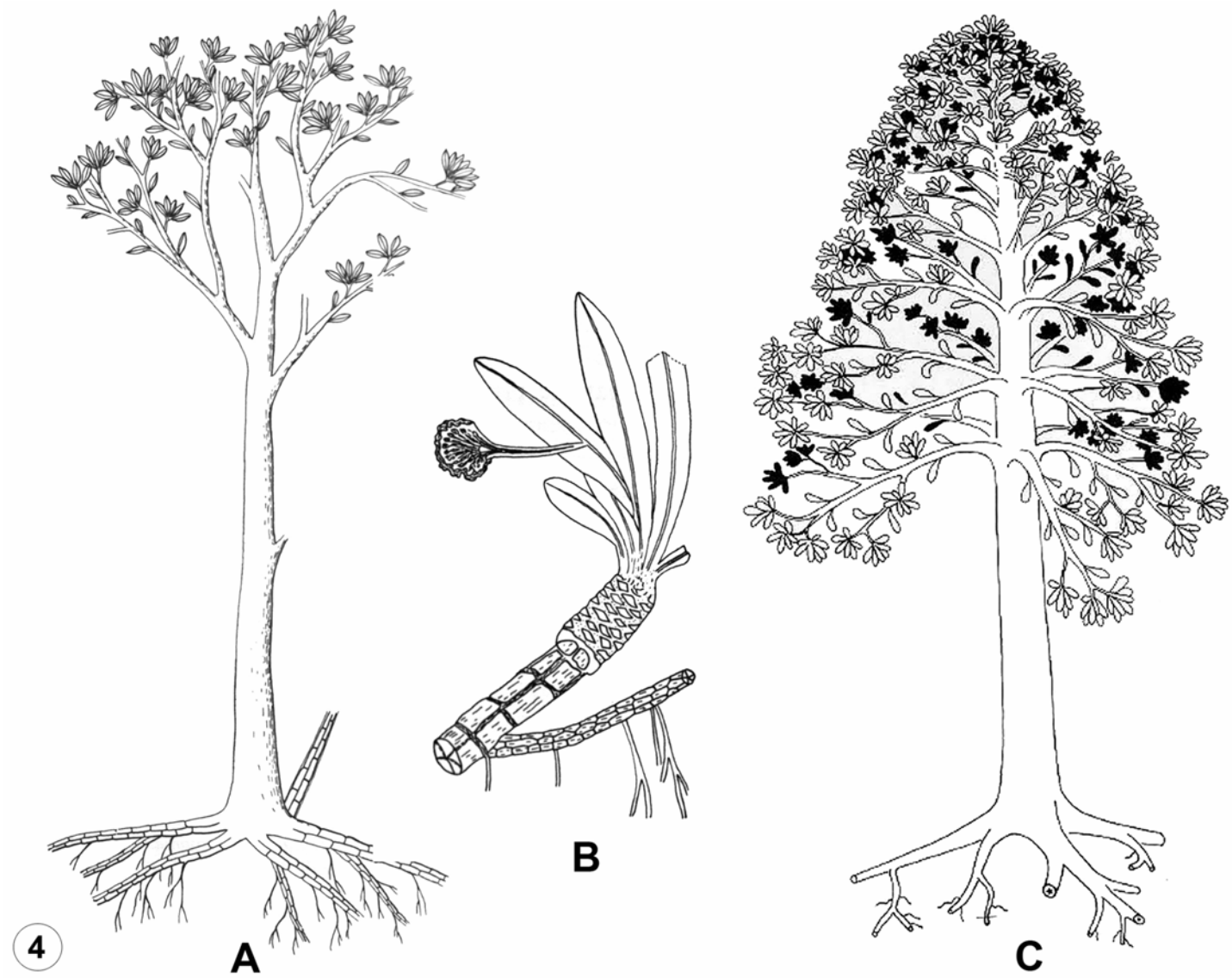
Plate 2 Fig. 4: Reconstructions of *Glossopteris* plant. A) Reconstruction from Pant and Singh, 1974. B) Reconstruction from Pant, 1962 showing *Vertebraria* root, stem with leaves attached in a whorl and a *Scutum*) reproductive structure. C) Reconstruction from Gould and Delevoryas, 1977.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A
B
C

Plate 3 Figs. 5-8 Impressions of glossopterid ovulate reproductive structures. Fig. 5: Multiovulate *Plumsteadia semnes* from Australia. University of Queensland (Geological Survey of Queensland) #GSQF5505. scale bar = 1 cm. Fig. 6: Multiovulate *Scutum leslii* attached to the midrib of a vegetative *Glossopteris* leaf (arrow). Bernard Price Institute #BP-2-13739. scale bar = 2 cm. Fig. 7: Pedicellate megasporophyll *Lidgettonia africana* with petiole towards left and apex towards right. Two "cupules" are attached to a megasporophyll (scale leaf). Bernard Price Institute #BP-2-8334. scale bar = 1 cm. Fig. 8: *Rigbya arberioides* showing a long petiole which dichotomizes at the tip and bears terminal, uniovulate cupules. Inset shows more detail of at least eight cupules. Bernard Price Institute #BP-2-8187a. scale bar = 1 cm. Inset scale bar = 50 mm.

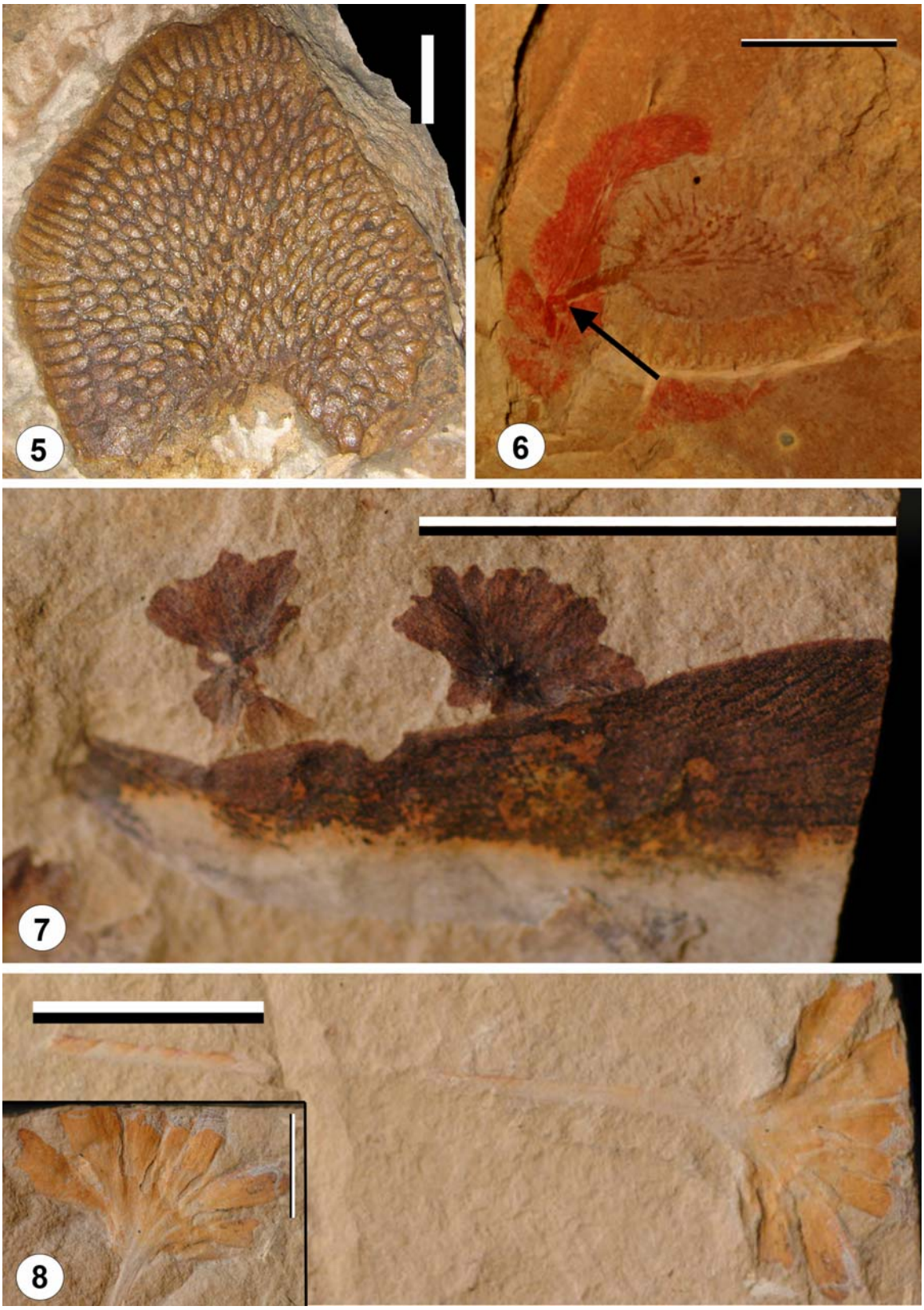
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Plate 4 Figs. 9-10 Reconstruction from Plumstead (1956a) of a bivalved megasporophyll. Fig. 9: A) Pollination stage showing two separate cupule halves with the abaxial half containing unfertilized ovules and the adaxial half acting as a protective shield (modified from Plumstead, 1956a). B) The abaxial half of a bivalved sporophyll showing numerous ovules with a central portion representing the stigma, according to Plumstead, 1956a, Modified from Plumstead, 1956a. C) *Scutum leslii*, illustrating what Plumstead interpreted as ovules at time of preservation. The specimen actually represents a mold of seed cushions; the projections initially interpreted as stigmas are the points of ovule attachment. Modified from Plumstead, 1956a. Bernard Price Institute #BP-2-13750. scale bar = 1 cm. Fig 10: A) Post-pollination stage of a bivalved sporophyll, according to Plumstead. The adaxial and abaxial halves of the cupule are fused to protect maturing ovules (Modified from Plumstead, 1956a). B) The adaxial half of a sporophyll illustrating the swollen sacs that contain maturing ovules according to Plumstead (1956a) C) *Gladiopomum dutoitides*, illustrating the "swollen sacs" of Plumstead's maturing ovules. The specimen actually represents a cast of the seed cushions which occur as depressions in the sporophyll; each seed cushion bore a single ovule in life. Bernard Price Institute #BP-2-13754. scale bar = 1 cm.

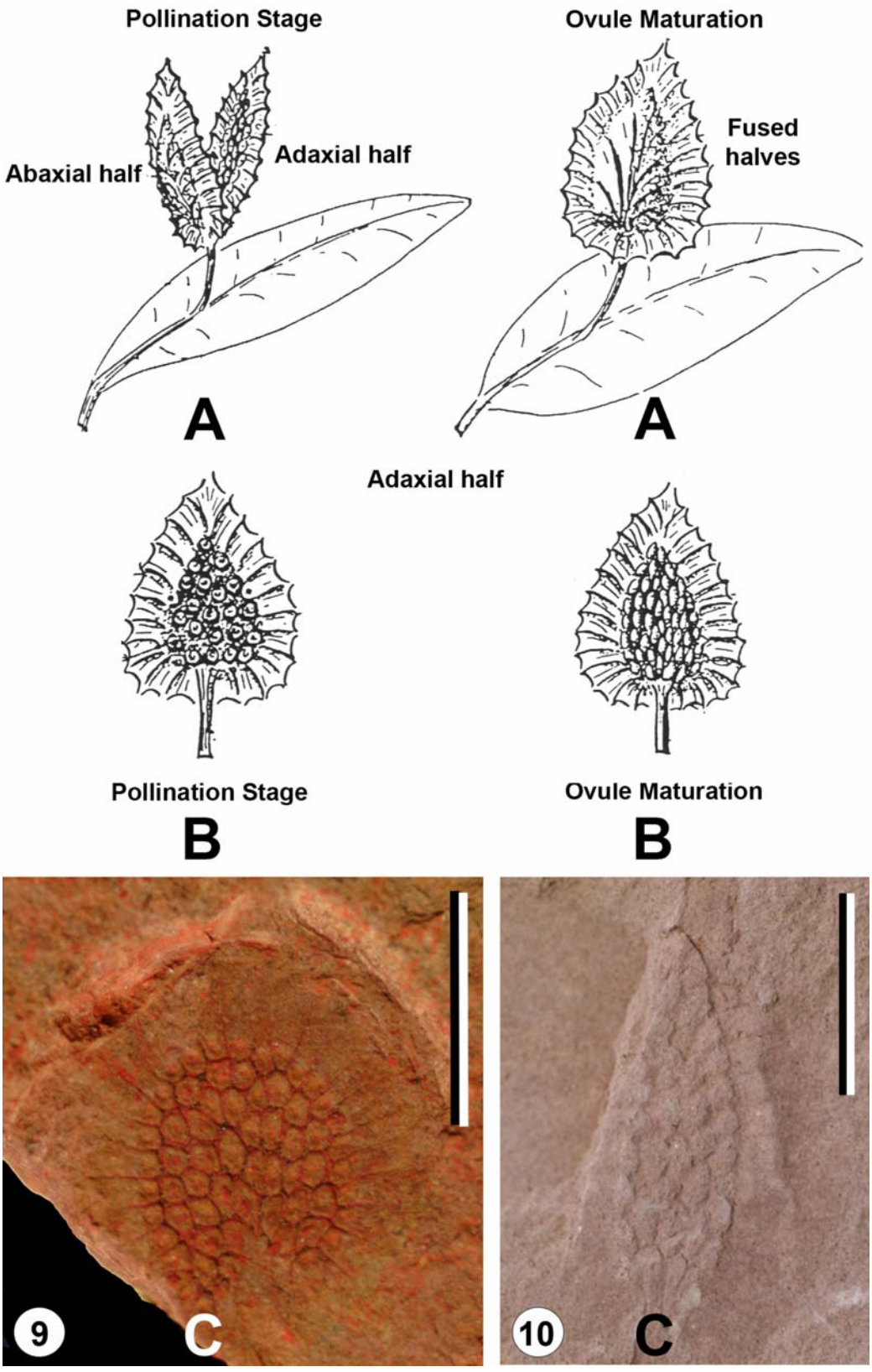
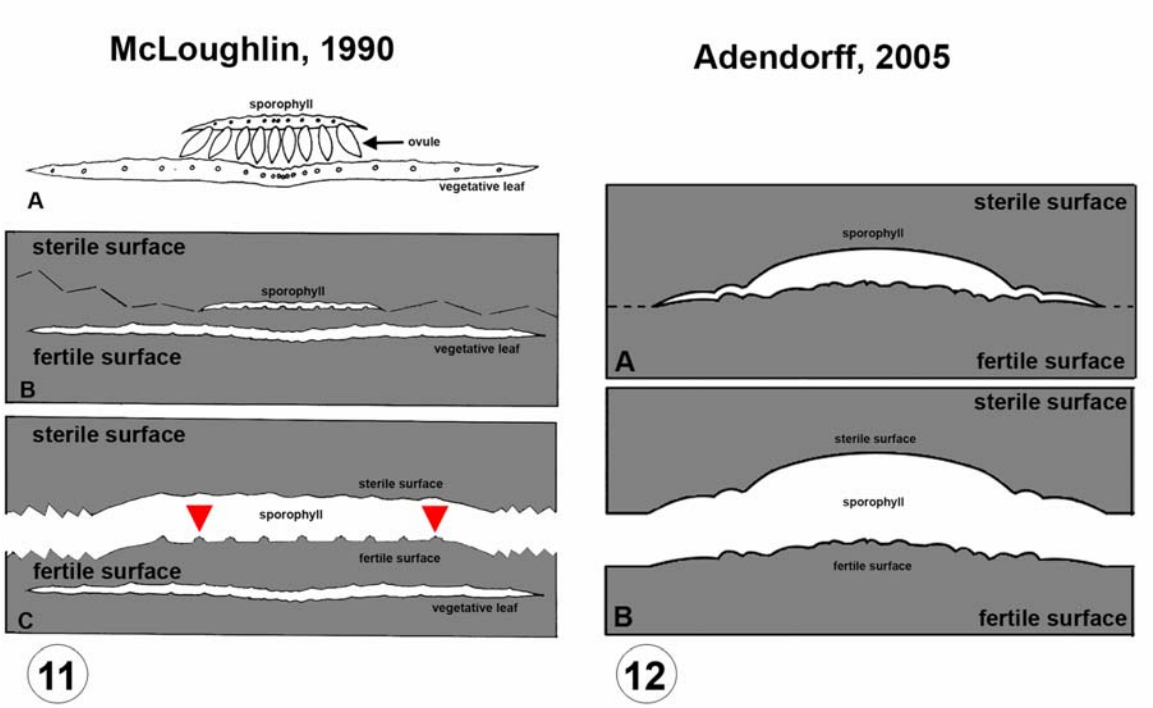
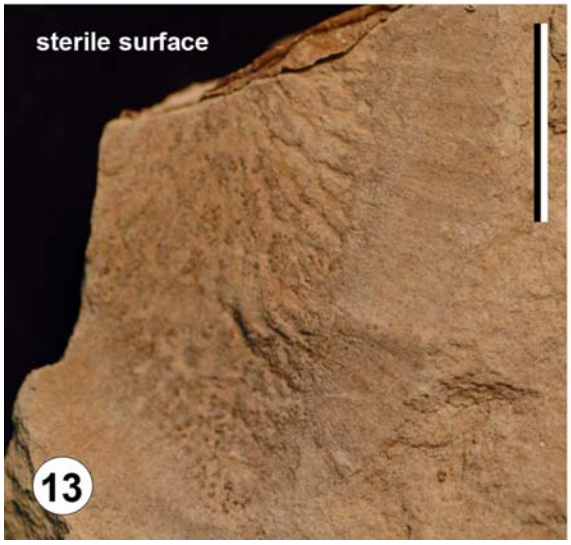

Pollination Stage
Ovule Maturation
Abaxial half
Adaxial half
Fused halves
A
A
Adaxial half
Pollination Stage
Ovule Maturation
B
B
9
C
10
C

Plate 5 Figs. 11-14 Interpretations of part and counterpart of impression specimens of glossopterid reproductive material. In Figs. 11 and 12, C is a higher magnification of B. Fig. 11: McLoughlin's (1990b) interpretation of a specimen split to reveal tubercles (Fig. 11C red arrowheads) on the fertile surface which represent the point of ovule attachment. Fig. 12: Prevec et al.'s (2008) and Adendorff's (2005) interpretation of part and counterpart of impression specimens with the part illustrating the so-called sterile surface of a megasporophyll and the counterpart illustrating the fertile surface. Fig. 13: *Scutum leslii* oriented with the apex of the sporophyll towards the base of the image to prevent the optical illusion that can occur in photographing glossopterid specimens. Specimen represents the so-called sterile part of a sporophyll. The problem with this interpretation is the presence of interrupted vasculature (projections) where ovules were attached and is addressed in Chapter 2. Bernard Price Institute #BP-2-13845. scale bar = 1 cm. Fig. 14: *Scutum leslii* oriented with the apex towards the bottom to prevent an optical illusion. This specimen is the counterpart to Fig. 13 and represents the fertile surface of a sporophyll with projections (cast of seed cushions) observed towards the apex of the specimen. Bernard Price Institute #BP-2-13733. scale bar = 1 cm.


McLoughlin, 1990
sporophyll
ovule
vegetative leaf
A
sterile surface
sporophyll
fertile surface
vegetative leaf
B
sterile surface
sterile surface
sporophyll
fertile surface
fertile surface
vegetative leaf
C
11
Adendorff, 2005
sterile surface
sporophyll
A
fertile surface
sterile surface
sterile surface
sporophyll
fertile surface
B
fertile surface
12


sterile surface
13

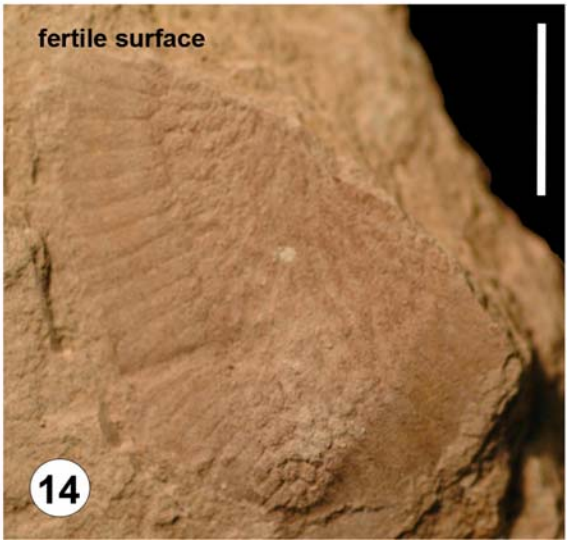

fertile surface
14

Plate 6 Figs. 15-17 Plumstead's (1956a) misinterpretation of ovule development. Fig. 15 A) Her interpretation of the abaxial surface of the megasporophyll with ovules at the time of pollination. From Plumstead 1956a B) Enlarged view of ovules during time of pollination showing a raised surface with either a depression or projection (depending on angle of photograph - see Plate 7) in center interpreted as the stigma. C) *Gonophylloides waltonii* showing projections with a depression in the center of each. The specimen represents a cast of seed cushions with the central depression representing the point of ovule attachment. Bernard Price Institute #BP-2-14239a. scale bar = 1 cm. Fig 16: A) Plumstead's interpretation of the abaxial surface of the megasporophyll showing 'sacs' with maturing ovules inside. B) Enlarged view of sacs illustrating swollen surface of specimen. C) *Scutum leslii* showing cast of seed cushions without the presence of projections or depressions, rather than the 'sacs' with developing ovules of Plumstead. Bernard Price Institute #BP-2-13870. scale bar = 1 cm. Fig. 17: A) Same image as Fig. 15A illustrating the fertile half of a mature sporophyll. From Plumstead 1956a. B) Plumstead's interpretation of a megasporophyll after the ovules have been dispersed showing depressions in the center of each circular projection Interpreted as sacs surrounding developing ovules have burst and released the seed. C) *Gonophylloides waltonii* illustrating Plumstead's interpretation. The specimen represents a cast of seed cushions rather than burst seed sacs and is the counterpart to Fig. 15C. Bernard Price Institute #BP-2-14239b. scale bar = 1 cm.

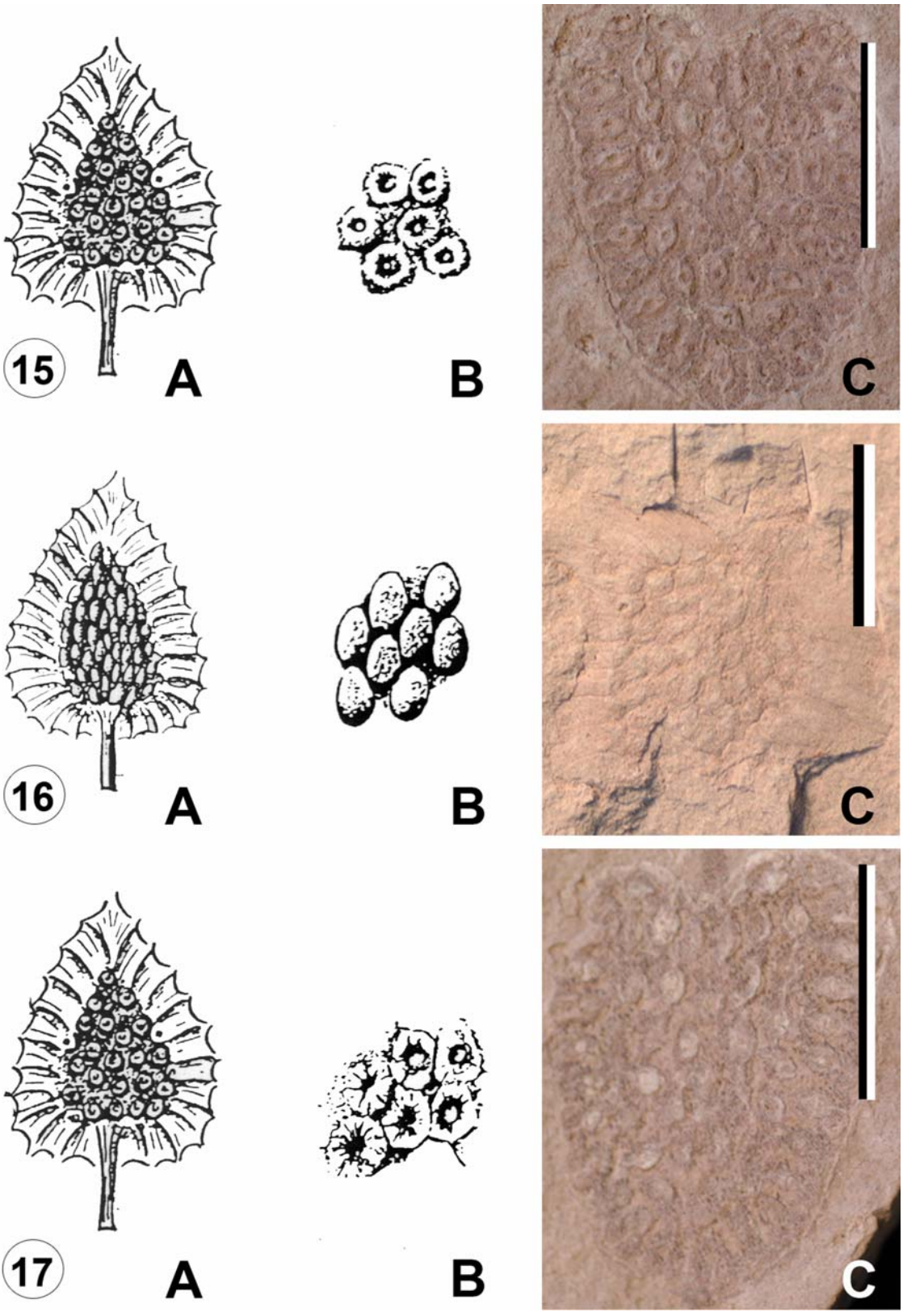

15
A
B
C
16
A
B
C
17
A
B
C

Plate 7 Figs. 18-22 Optical illusion in interpretation of megasporophyll orientation. Fig. 18: *Plumsteadia ovata* with the apex of the specimen toward the right. The depressions on the surface of the specimen represent seed cushions. KU #PM1912a. scale bar = 2 mm. Fig. 19: The same specimen in Fig. 18 rotated 180°. The depressions in Fig. 18 now appear as projections. The surface of the specimen actually contains depressions as seen in Fig. 18. KU #PM1912a. scale bar = 2 mm . Fig. 20: Image from Plate 2 fig. 2 of Plumstead (1956a) in originally published orientation. Sporophyll appears to have depressions (seed cushions) with projections in the center (point of ovule attachment). Fig. 21: Fig. 20 rotated 90° clockwise with depressions now appearing as projections. Fig. 22: Image of the specimen shown in Figs. 20-21 taken in 2008 showing that the surface of specimen contains projections and not depressions as originally interpreted in Plumstead's (1956a) publication. Bernard Price Institute #BP-2-13736a. scale bar = 2 cm.

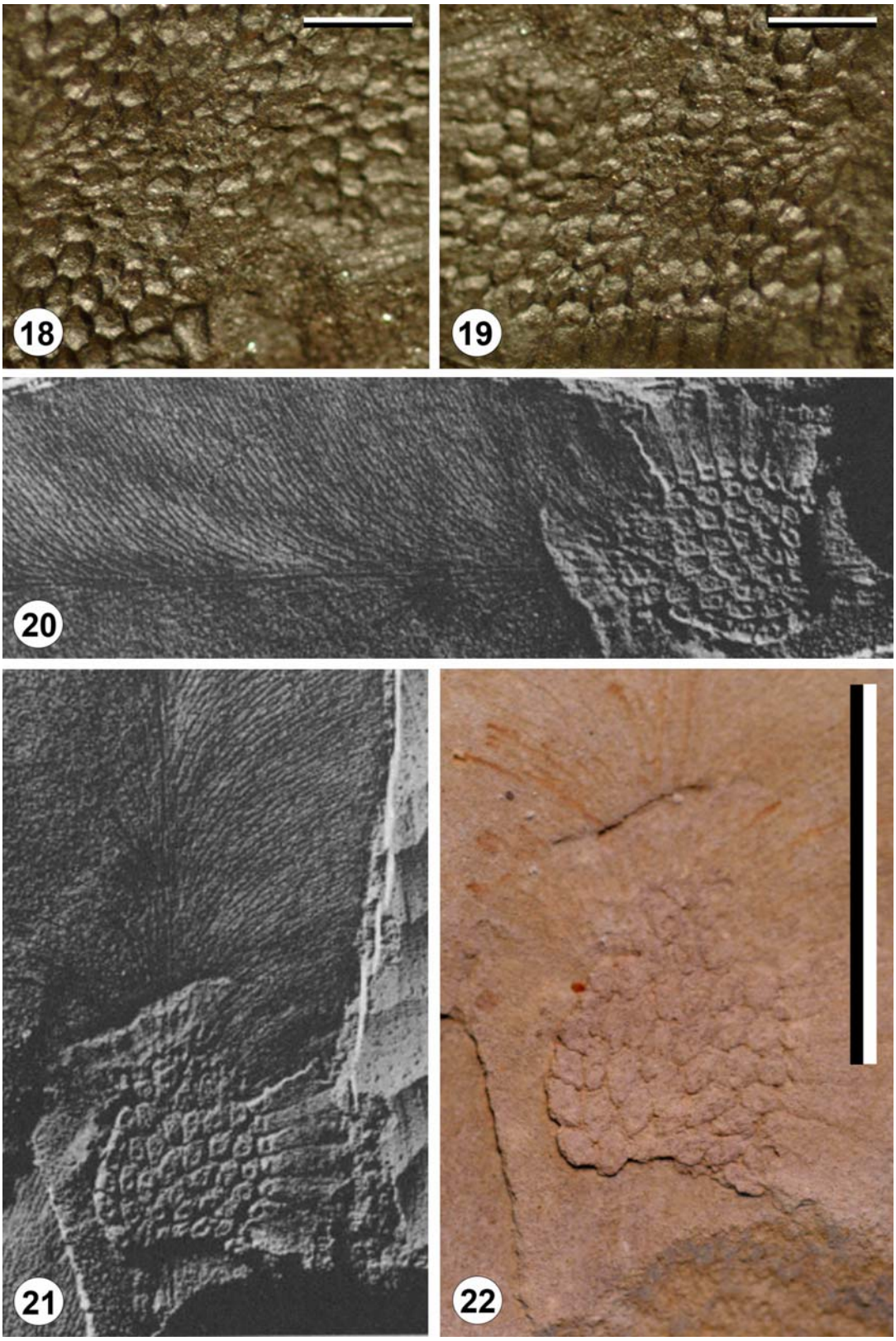

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Plate 8 Figs. 23-26. Geography and Stratigraphy of this study. Fig. 23: Map of Antarctica and the Transantarctic Mountains. Localities indicated by blue dots. (Modified from Elliot et al., 2006) Fig. 24 Stratigraphy of the Beacon Supergroup in the Beardmore Glacier region of the Central Transantarctic Mountains. Red line indicates approximate position of fossils in the strata. (Modified from E.L. Taylor et al., 1989) Fig. 25: Stratigraphy of the Beacon Supergroup in the Allan Hills region of Southern Victoria Land. The red line indicates the approximate position of the fossils in the strata. (Modified from Elliot et al., 2006) Fig. 26: Stratigraphy of the Beacon Supergroup at the Mt. Schopf and Mt. Glossopteris localities of the Horlick Mountains. The red line indicates the approximate position of the fossils in the strata. (Modified from Long, 1964)

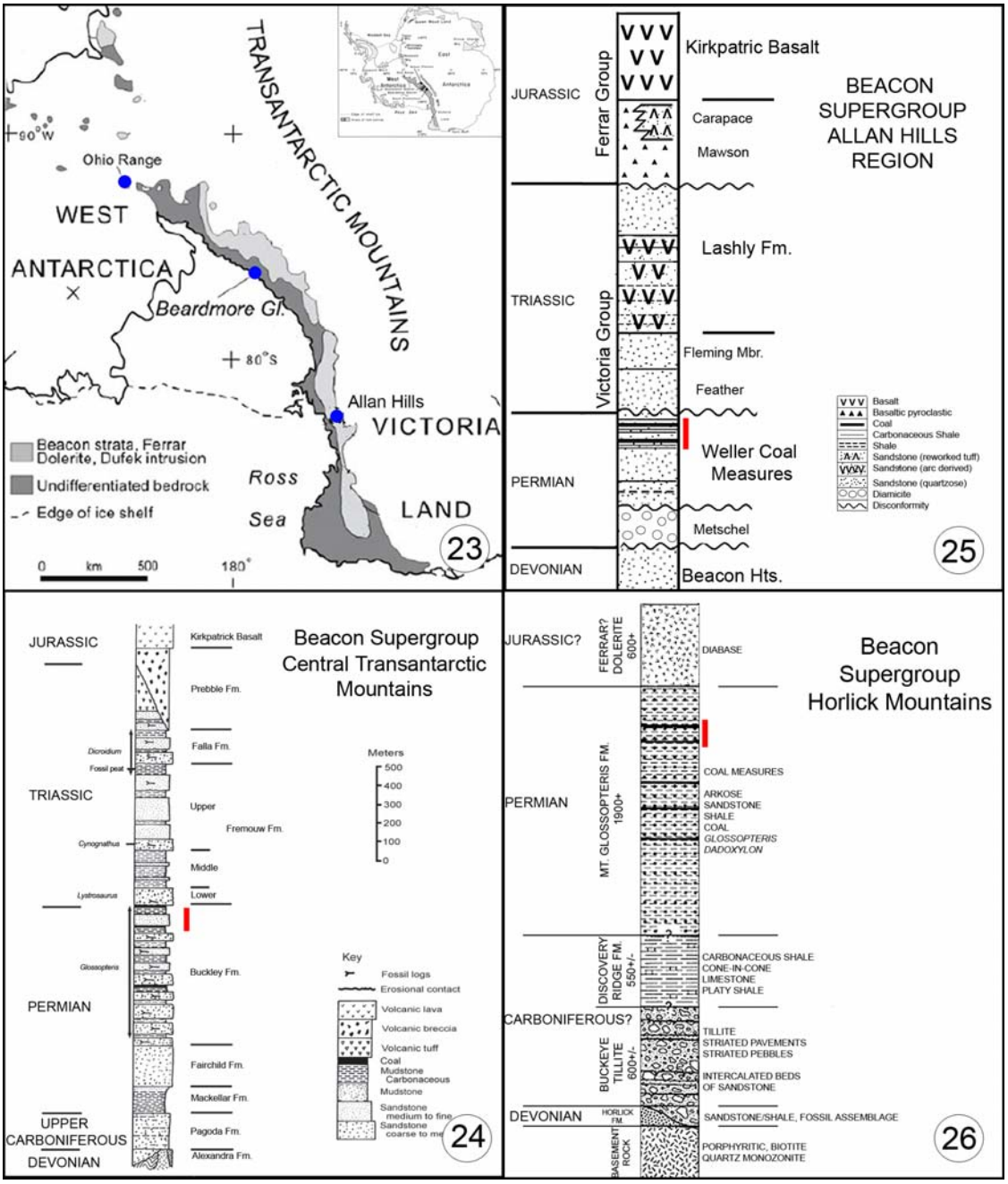
TRANSANTARCTIC MOUNTAINS
60°W
Ohio Range
WEST
ANTARCTICA
Beardmore Gl.
80°S
Allan Hills
VICTORIA
LAND
Ross
Sea
Beacon strata, Ferrar Dolerite, Dufek intrusion
Undifferentiated bedrock
Edge of ice shelf
0 km 500
180°
23
JURASSIC
TRIASSIC
PERMIAN
DEVONIAN
Ferrar Group
Victoria Group
Kirkpatric Basalt
Carapace
Mawson
Lashly Fm.
Fleming Mbr.
Feather
Weller Coal Measures
Metschel
Beacon Hts.
BEACON SUPERGROUP ALLAN HILLS REGION
Basalt
Basaltic pyroclastic
Coal
Carbonaceous Shale
Shale
Sandstone (reworked tuff)
Sandstone (arc derived)
Sandstone (quartzose)
Diamicite
Disconformity
25
JURASSIC
TRIASSIC
PERMIAN
UPPER CARBONIFEROUS
DEVONIAN
Kirkpatrick Basalt
Prebble Fm.
Falla Fm.
Upper
Fremouw Fm.
Middle
Lower
Buckley Fm.
Fairchild Fm.
Mackellar Fm.
Pagoda Fm.
Alexandra Fm.
Dicroidium
Fossil peat
Cynognathus
Lystrosaurus
Glossopteris
Beacon Supergroup Central Transantarctic Mountains
Meters
500
400
300
200
100
0
Key
Fossil logs
Erosional contact
Volcanic lava
Volcanic breccia
Volcanic tuff
Coal
Mudstone Carbonaceous
Mudstone
Sandstone medium to fine
Sandstone coarse to me
24
JURASSIC?
PERMIAN
CARBONIFEROUS?
DEVONIAN
FERRAR? DOLERITE 600+
MT. GLOSSOPTERIS FM. 1900+
DISCOVERY RIDGE FM. 550+/-
BUCKEYE TILLITE 600+/-
HORLICK FM
BASEMENT ROCK
DIABASE
COAL MEASURES
ARKOSE
SANDSTONE
SHALE
COAL
GLOSSOPTERIS
DADOXYLON
CARBONACEOUS SHALE
CONE-IN-CONE
LIMESTONE
PLATY SHALE
TILLITE
STRIATED PAVEMENTS
STRIATED PEBBLES
INTERCALATED BEDS OF SANDSTONE
SANDSTONE/SHALE, FOSSIL ASSEMBLAGE
PORPHYRITIC, BIOTITE QUARTZ MONZONITE
Beacon Supergroup Horlick Mountains
26

Plate 9 Figs. 27-31, *Plumsteadia ovata*. Fig. 27: Cast of the fertile surface of the megasporophyll. The apex of the sporophyll is to the left, the base to the right. Darker spots on the specimen indicate the positions of ovule attachment to the sporophyll; arrows point to three of these. PM-3-16. scale bar = 1 cm. Fig. 28: Depressions representing molds of the seed cushions on the laminar megasporophyll. No ovules are present on the sporophyll. The base of the sporophyll is at the bottom of the picture with the apex towards the top. PM1912a. scale bar = 2 cm. Fig. 29: Counterpart of Fig. 28 showing casts of seed cushions. No ovules are present. Orientation of sporophyll is the same as in Fig. 28. PM1912b. scale bar = 2 cm. Fig. 30: Large, dark circles are depressions that represent ovule cushions. Smaller circular area in the center of each circle indicates the point of ovule attachment. PM1937. scale bar = 2 mm. Fig. 31: Fluted, laminar morphology of the marginal wing. Edge of wing at the top of the image, center of the sporophyll towards the bottom of the image. Lines on wing indicate separation between two adjacent ovules (arrows). PM-3-22. scale bar = 2 mm.

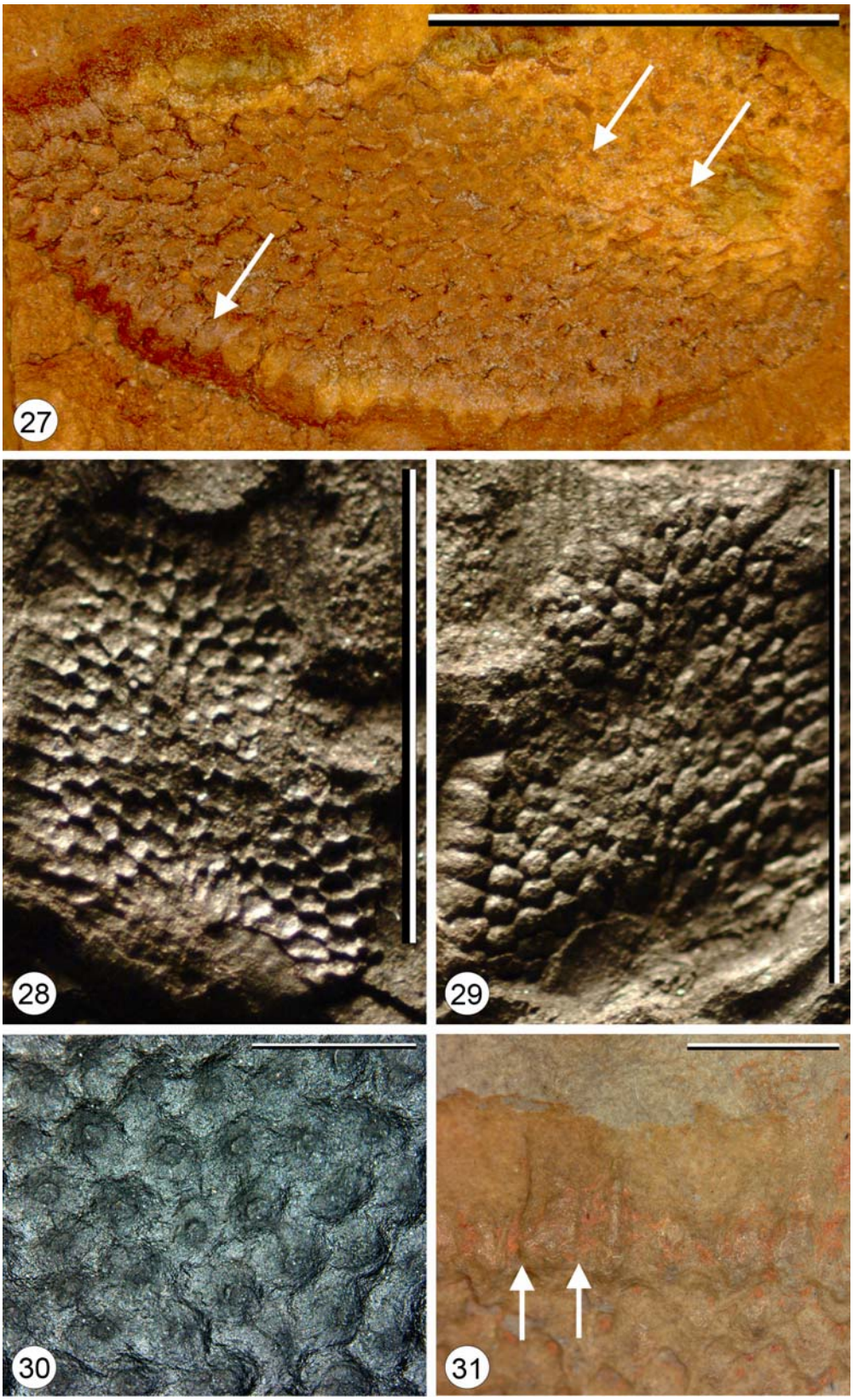
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Plate 10 Figs. 32-37. Figs. 32-33, *Plumsteadia ovata*; Figs. 34-37, *Rigbya chtenia*. Fig. 32: Individual seed cushion showing oval pit in the center where ovule was attached and striations radiating out from this pit (arrow). PM1912a. scale bar = 0.5 mm. Fig. 33: SEM of seed cushions (circular areas, right) with remains of some vasculature (lines, left). Base of sporophyll towards the left, apex to the right. PM1912a. scale bar = 1 mm. Fig. 34: Holotype of *Rigbya chtenia* showing pedicel terminating in several laminar structures which have overlapped during preservation. Associated ovule left of the sporophyll. PM2027. scale bar = 2 mm. Fig. 35: A single laminar cupule showing the constricted base and expanded fluted apex (white arrow). The presence of seed scar is seen towards the base of the lamina (black arrow). PM2027. scale bar = 1 mm. Fig. 36: Four stalks showing basal dichotomies and pedicel below. Each stalk bears a single cupule (arrows). PM2174. scale bar = 5 mm . Fig. 37: *Rigbya* showing basal attachment of ovules to cupules (arrow). Paratype PM2013. scale bar = 2 mm.

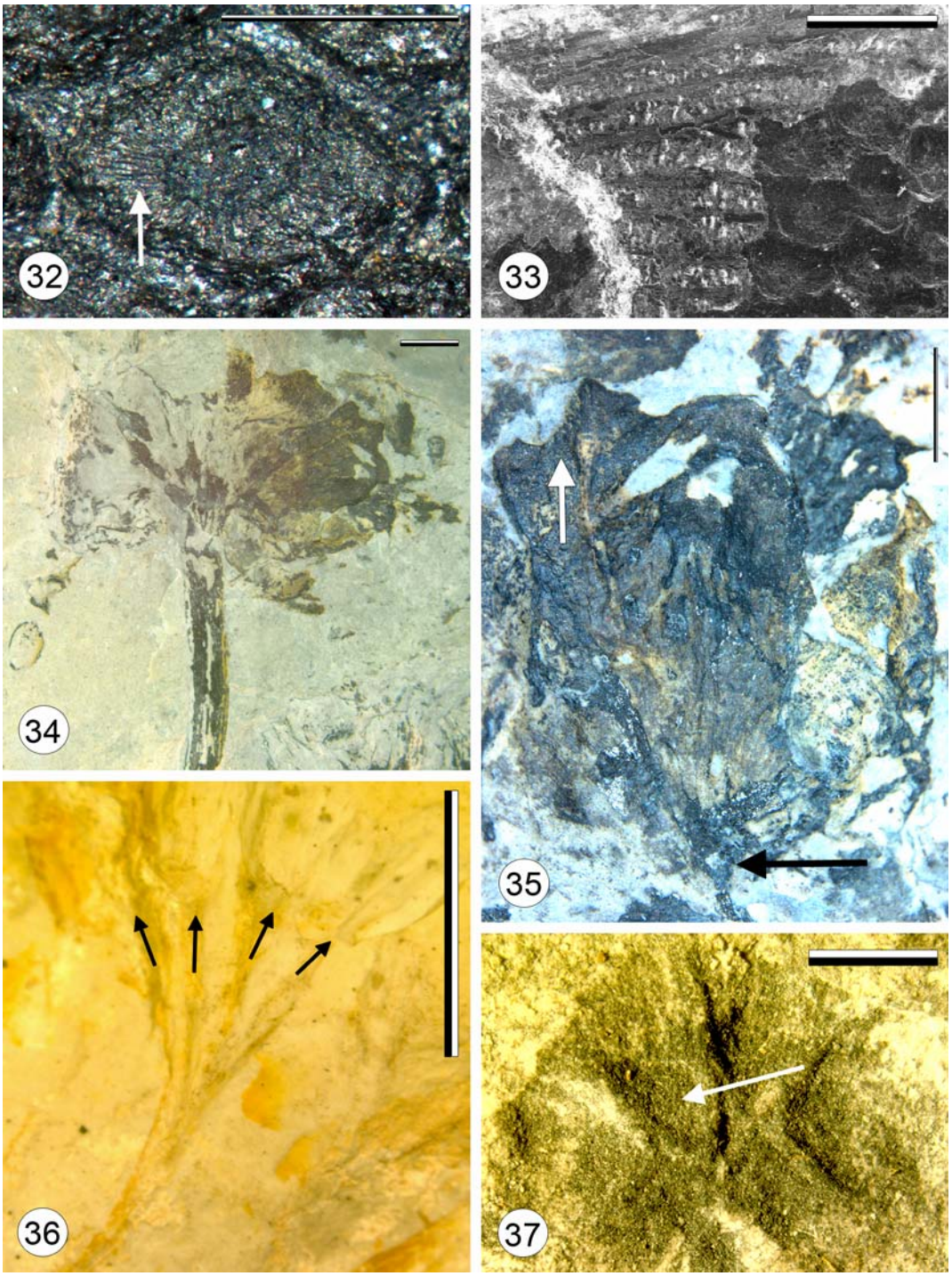
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Plate 11 Figs. 38-42. Figs. 38-40 *Eretmonia singulia*. Figs. 41-42 *Arberiella inflectada*. Fig. 38: Holotype of *Eretmonia singulia* from Antarctica. The microsporophyll bears two clusters of sporangia. The cluster on the right is partially separated from the sporophyll. PM2046b. scale bar = 2 mm. Fig. 39: Higher magnification of Figure 16 showing the pedicel (arrow) that dichotomizes to terminate in sporangia. PM2046b. scale bar = 1 mm. Fig. 40: Image of a single sporangium of *Eretmonia singulia* showing its elongate, bean-like shape. PM2046a. scale bar = 1 mm. Fig. 41: Holotype of *Arberiella inflectada* which consists of a cluster of sporangia unattached to a pedicel. PM2181b. scale bar = 2 mm. Fig. 42: Isolated sporangia of *A. inflectada* showing recurved base (arrows) and a bulbous apex. PM2181b. scale bar = 1 mm.

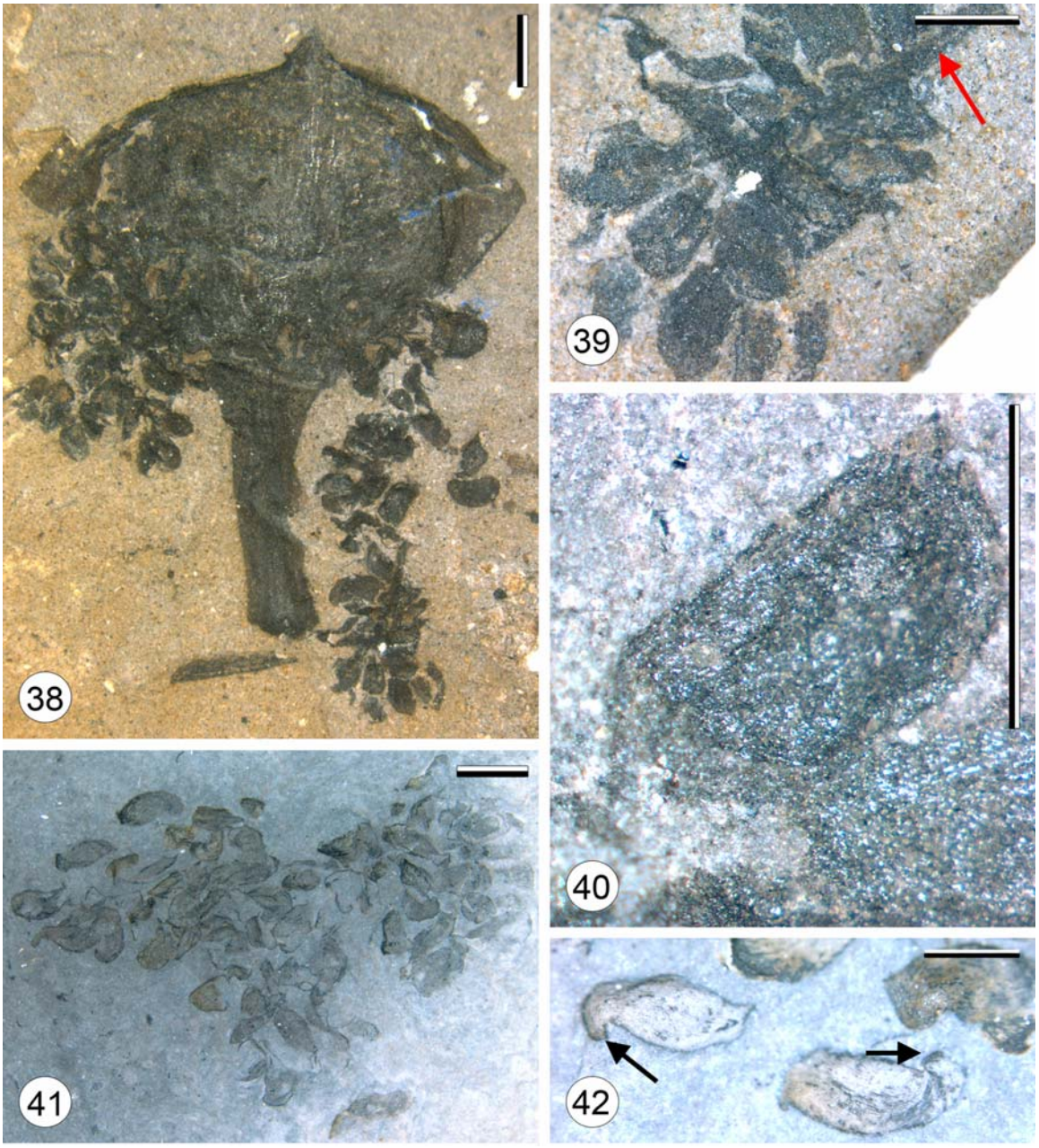
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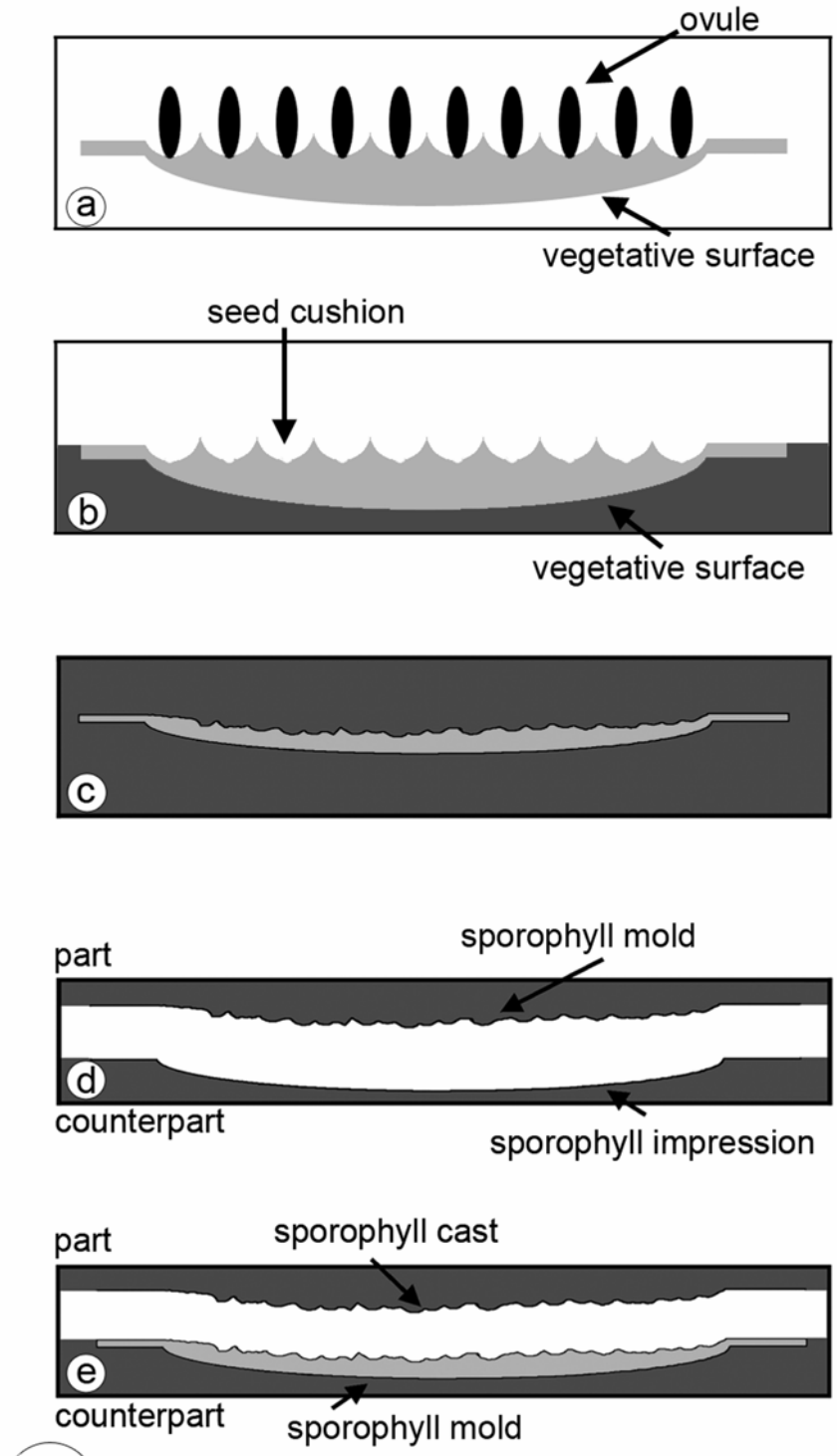
Plate 12 Fig. 43 Model of exposed impression surfaces. Fig. 43 Diagram of a cross section of a multiovulate megasporophyll from time of fertilization to splitting of fossil impression specimen showing part and counterpart. Figs. 43 c, d modified from Prevec et al., 2008. a) Megasporophyll at time of fertilization. Ovules (black) are attached to the sporophyll (light grey) in seed cushions and exposed for pollination. Projections on either side of the sporophyll represent the wing. b) Megasporophyll (light grey) at time of deposition. Ovules have been shed and only seed cushions remain on the fertile surface when it falls into the sediment. c) Megasporophyll (light grey) after compression in the matrix before the specimen is split. The vegetative surface of the sporophyll is on the bottom and the remains of the seed cushions are on top. d) Split specimen showing the sporophyll mold ('fertile' surface of Prevec et al., 2008) and the sporophyll impression ('sterile' surface of Prevec et al., 2008). The rock split through the sporophyll showing vasculature on the sporophyll impression and the underside of seed cushions on the sporophyll mold. Comparable to specimens from South Africa shown in Figs. 44-45. e) Specimen split showing the sporophyll cast (light grey; 'fertile' surface of Prevec et al., 2008) and the sporophyll mold ('sterile' surface of Prevec et al., 2008). The rock split showing a mold where seed cushions were located and projections representing a cast of the seed cushions. Comparable to Antarctic specimens shown in Figs. 28-29 and South African specimens in Figs. 46-47.


ovule
a
vegetative surface
seed cushion
b
vegetative surface
c
part
sporophyll mold
d
counterpart
sporophyll impression
part
sporophyll cast
e
counterpart
sporophyll mold

43

Plate 13 Figs. 44-47 *Gonophylloides strictum* from South Africa, Fig 44: Impression of the "sterile" surface (sporophyll impression) showing uninterrupted vasculature across the entire sporophyll. BP-2-14223b. scale bar = 1 cm. Fig. 45: Counterpart of Fig 44. "Fertile" surface (sporophyll mold) with vasculature interrupted by pits in the location of the seed cushions (arrows). BP-2-14225. scale bar = 1 cm. Fig. 46: Impression of the "sterile" surface (sporophyll mold) with the pits in the location of seed cushions (arrows). Fig. 47: Counterpart of Fig. 46 with the "fertile" surface (sporophyll cast) indicated by projections (arrows) in the location of the seed cushions. BP-2-14231b. scale bar = 1 cm.

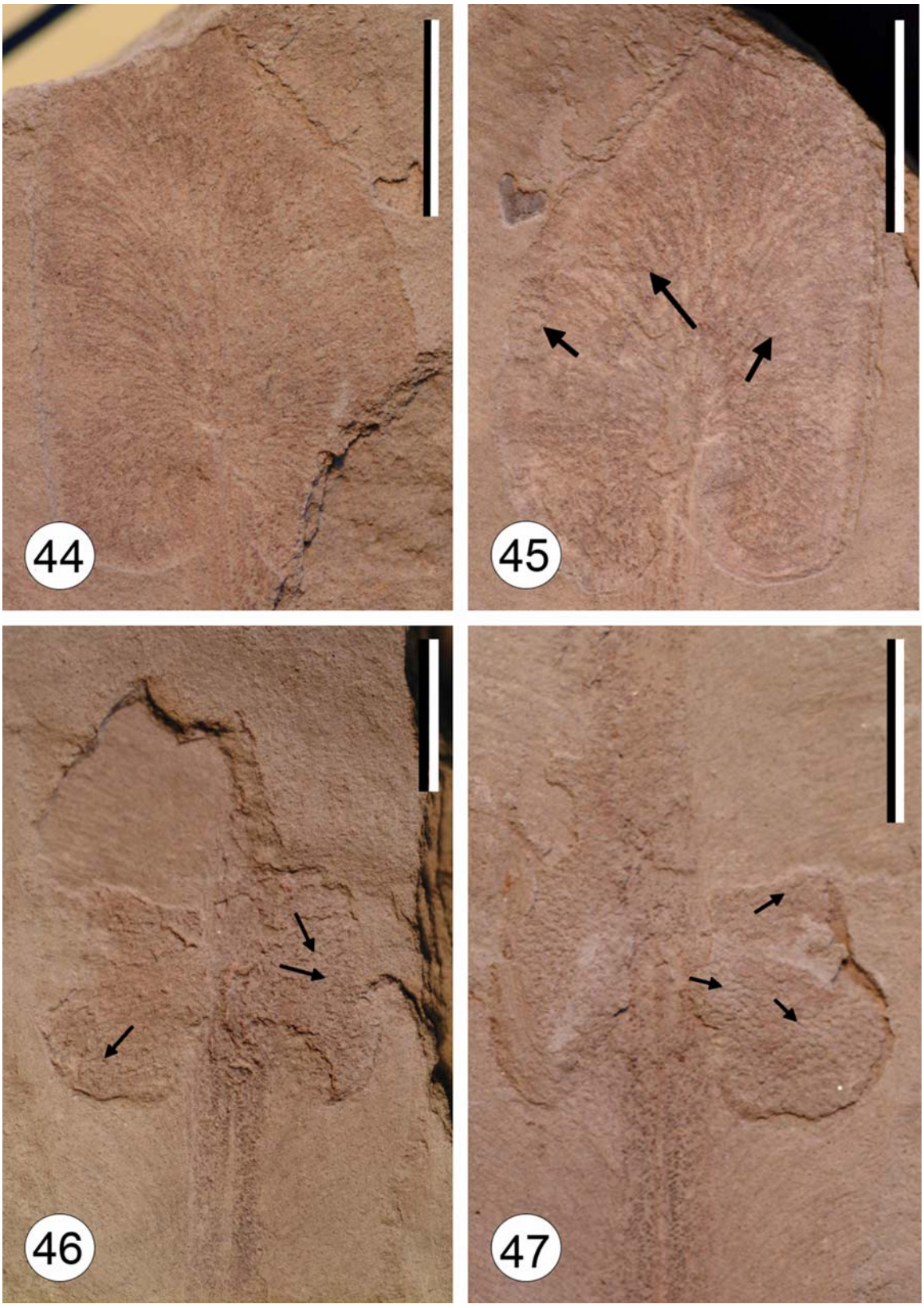

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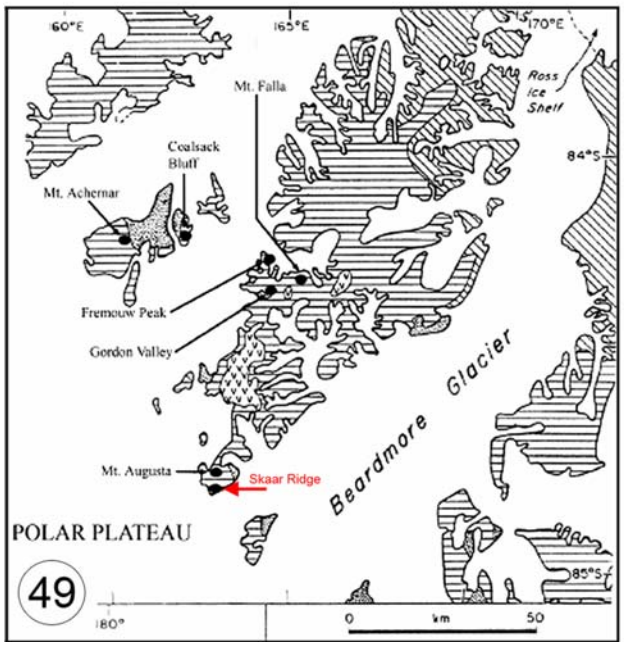
Plate 14 Figs. 48-50. Collection locality and stratigraphy. Fig. 48: Locality of fossils used in this study are highlighted in red; *Arberiella* of Cridland (1963) is in green, and *Arberiella* of Lindström et al. (1997) is in blue. Fig. 49: Skaar Ridge locality in the Transantarctic Mountains where specimens of *Lakkosia kerasata* and *Arberiella schopfii* were collected. Fig. 50: Stratigraphy of the Beacon Supergroup in the Beardmore Glacier region of the Central Transantarctic Mountains. Red line indicates approximate position of fossils in the strata. (Modified from E.L. Taylor et al., 1989).


Queen Maud Land
Weddell Sea
Theron Mts.
Whichaway Nunataks
Prince Charles Mts.
East
Pensacola Mts.
Nilsen Plateau
Ellsworth Mts.
Ohio Range
West Antarctica
Transantarctic Mts.
Antarctica
Shackleton Glacier
Beardmore Glacier
Disch Promontory
Ross Sea
Victoria Land
Horn Bluff
48


Mt. Falla
Ross Ice Shelf
Coalsack Bluff
Mt. Achernar
Fremouw Peak
Gordon Valley
Beardmore Glacier
Mt. Augusta
Skaar Ridge
POLAR PLATEAU
49
0
km
50

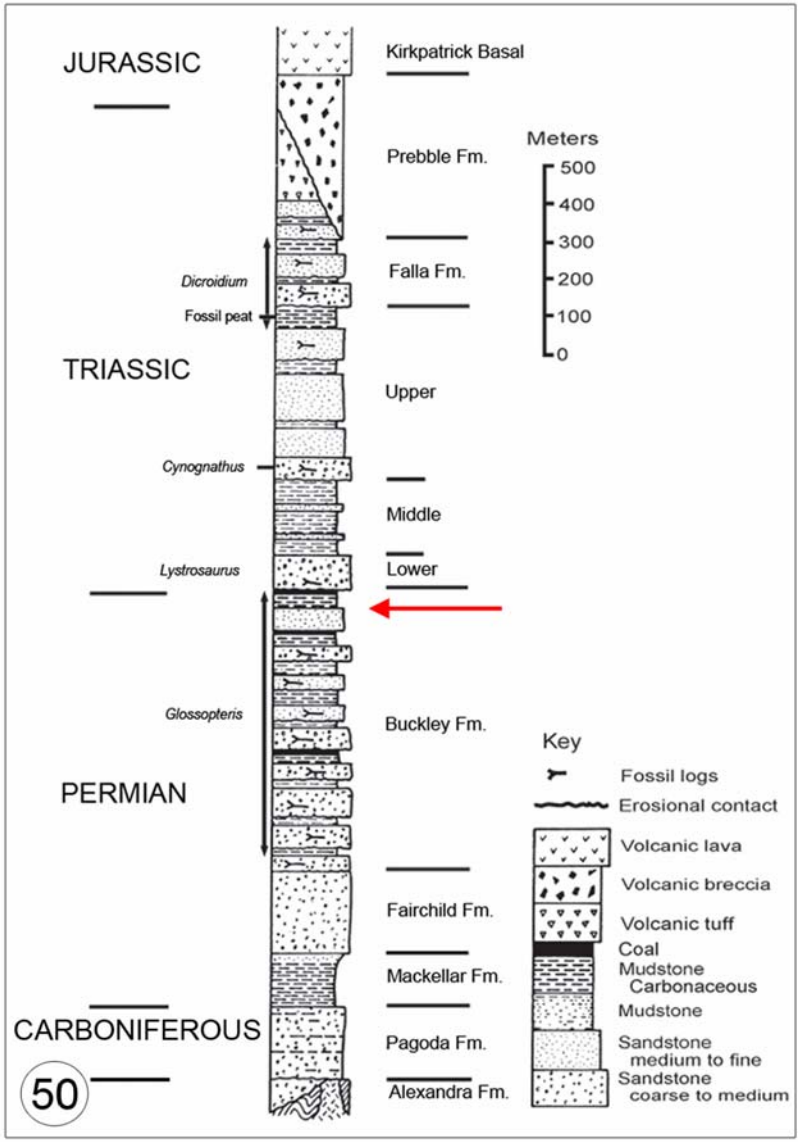
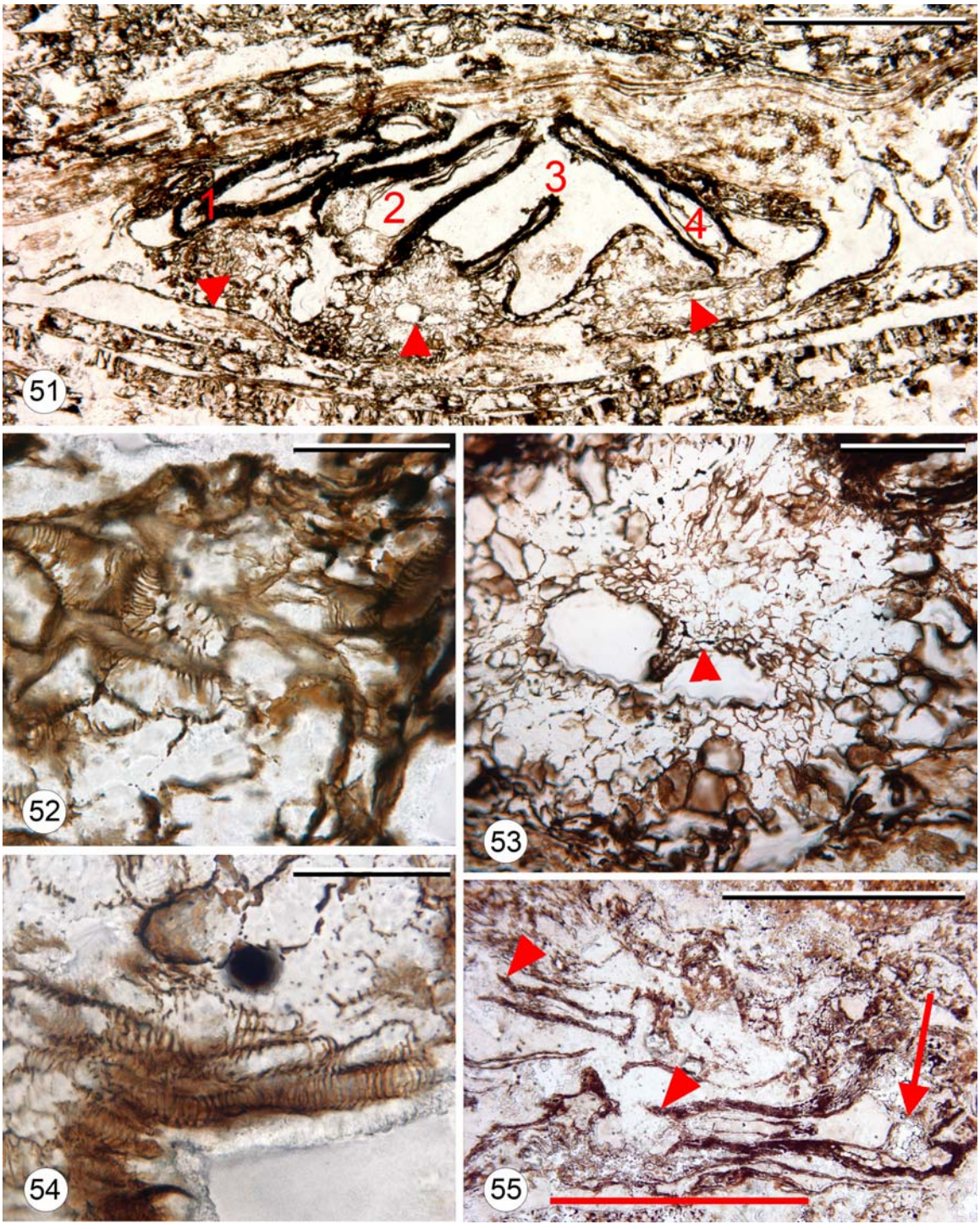

JURASSIC
TRIASSIC
PERMIAN
CARBONIFEROUS
Kirkpatrick Basal
Prebble Fm.
Falla Fm.
Upper
Middle
Lower
Buckley Fm.
Fairchild Fm.
Mackellar Fm.
Pagoda Fm.
Alexandra Fm.
Dicroidium
Fossil peat
Cynognathus
Lystrosaurus
Glossopteris
Meters
500
400
300
200
100
0
Key
Fossil logs
Erosional contact
Volcanic lava
Volcanic breccia
Volcanic tuff
Coal
Mudstone Carbonaceous
Mudstone
Sandstone medium to fine
Sandstone coarse to medium
50

Plate 15 Figs. 51-55 *Lakkosia kerasata* gen. et sp. nov. Fig. 51: Cross section through the sporophyll and longitudinal section through four ovules (numbered). Vascular bundles indicated by arrowheads. Ovule #2 is detached and turned 180° with the micropylar end facing the sporophyll. Holotype slide 7837 (13676 D-bot series δ peel 59). scale bar = 2 mm. Fig. 52: Oblique cross section of megasporophyll showing mesophyll with scalariform thickenings in transfusion tissue. Holotype slide 7837 (13676 D-bot series δ peel 59). scale bar = 0.05 mm. Fig. 53: Cross section through a vascular bundle. Xylem adaxial (arrow) and phloem lacuna abaxial. Holotype slide 7837 (13676 D-bot series δ peel 59). scale bar = 0.2 mm. Fig. 54: Oblique longitudinal section through xylem tracheids with scalariform thickenings. Paratype slide 15773 (13676 D-bot series β peel 120). scale bar = 0.05 mm. Fig 55: Oblique longitudinal section through two ovules showing broad bases (arrowheads). Micropyle of top ovule is to the right, but not in this plane of section. Compare to ovule #1 in fig. 1A. Micropyle of lower ovule at arrow. Sporophyll that ovules are attached to is just above the red line. Poor preservation does not show the attachment of the top ovule and most of the lower ovule to the sporophyll. Paratype slide 26460 (13676 E-top series r peel 28). scale bar = 1mm.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52
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55

Plate 16 Figs. 56-60 *Lakkosia kerasata* gen. et sp. nov. Fig. 56: Slightly oblique cross section through three ovules (numbered) showing the tight arrangement of ovules on the sporophyll. Ovules 1 and 3 each show the two hemispherical pads of parenchymatous tissue that surround the micropyle (see also fig. 51) and the distorted wings on either side. Ovule 2 shows a section below the micropylar parenchyma masses and appears compressed. Paratype slide 26393 (13676 E-top series q peel 30). scale bar = 1 mm. Fig. 57: Oblique cross section of an ovule surrounded by a thin strip of tissue (arrowheads) indicating the presence of an enclosing tissue around ovules. Paratype slide 12924 (13676 D-bot series β peel 52). scale bar = 0.5 mm. Fig. 58: Oblique longitudinal section of two poorly preserved ovules (O) showing the ovules enclosed in thin strips of tissue (arrows). Paratype slide 7852 (13676 D-bot series β peel 78). scale bar = 1 mm. Fig. 59: Longitudinal section through the secondary plane of an ovule showing the pads of tissue formed from the sclerotesta (p) and the micropyle in the center. The overarching tissue of the sarcotesta is poorly preserved and appears as thick black segments above the parenchymatous pads. The nucellus (N) is not attached to the integument. Holotype slide 7837 (13676 D-bot series δ peel 59). scale bar = 0.5 mm. Fig. 60: Oblique cross section of an ovule showing the outer sarcotesta (Sa), which forms the wings, and the sclerotesta (Sc), which forms the single parenchyma mass shown in this section. Paratype slide 7849 (13676 D-bot series δ peel 99). scale bar = 0.5mm.

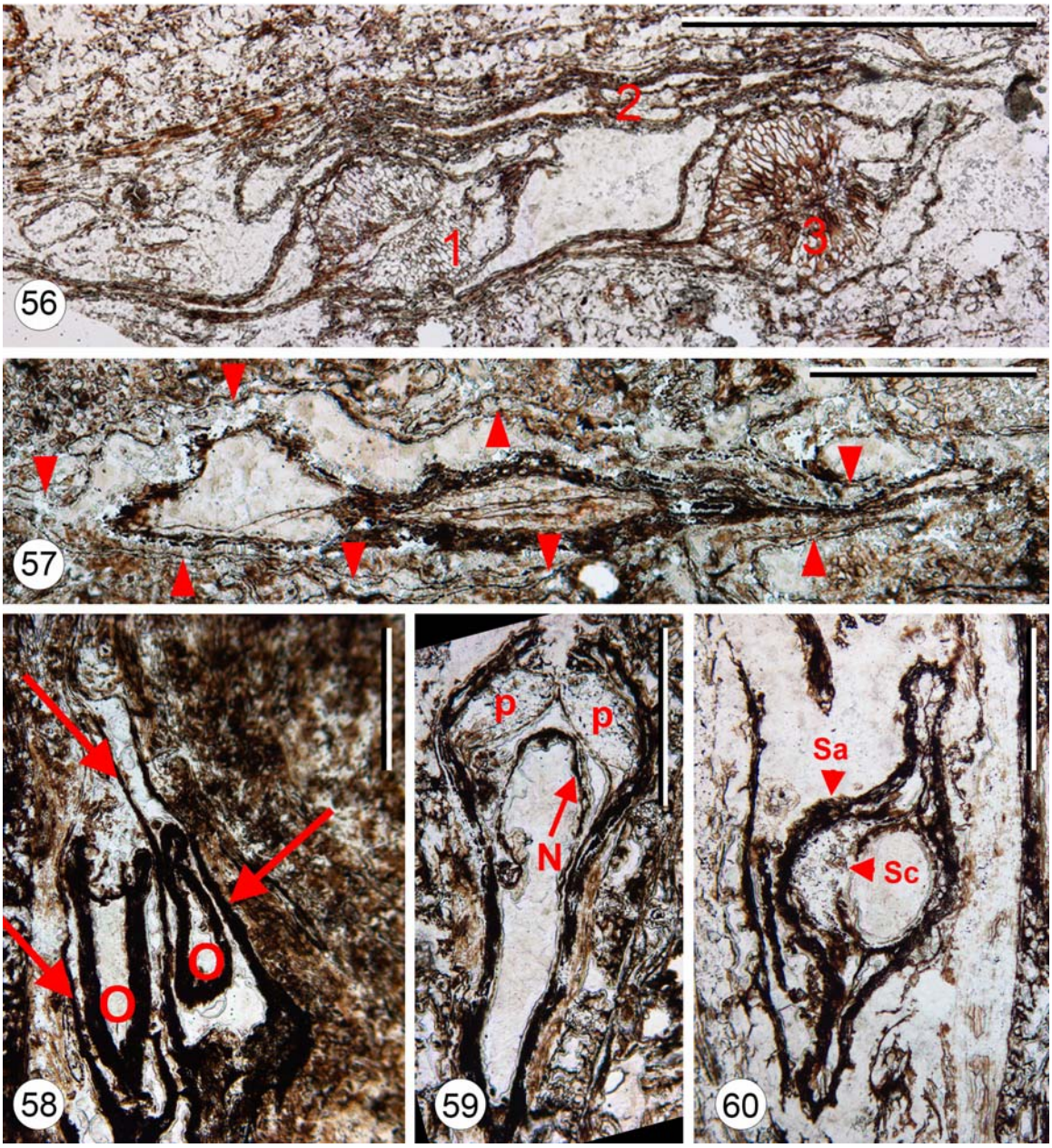
56
1
2
3
57
58
O
O
59
p
p
N
60
Sa
Sc

Plate 17 Figs. 61-64 *Lakkosia kerasata* gen. et sp. nov. Fig. 61: Oblique cross section of the micropylar end of an ovule. The two appressed hemispheres of parenchyma tissue form the micropyle (arrowhead). Paratype slide 26393 (13676 E-top series q, peel 30). scale bar = 0.5 mm. Fig. 62: Longitudinal section of the micropylar end of an ovule. The sclerotesta forms the two pads of tissue that form the central micropyle (M). The sarcotesta forms the overarching tissue (S) creating a presumed pollen capture region above the micropyle. Paratype slide 12924 (13676 D-bot series β peel 52). scale bar = 0.5mm. Fig. 63: Longitudinal section of an ovule showing the remnants of the nucellus (N) free from the integument except at the base. Holotype slide 7837 (13676 D-bot series δ peel 59). scale bar = 0.5 mm. Fig. 64: Longitudinal section of an ovule with *Protohaploxypinus* pollen in both the pollen capture region outside the micropyle (upper arrowhead) and the pollen chamber itself (lower arrowhead). Holotype slide 7840 (13676 D-bot series δ peel 66). scale bar = 0.5 mm.

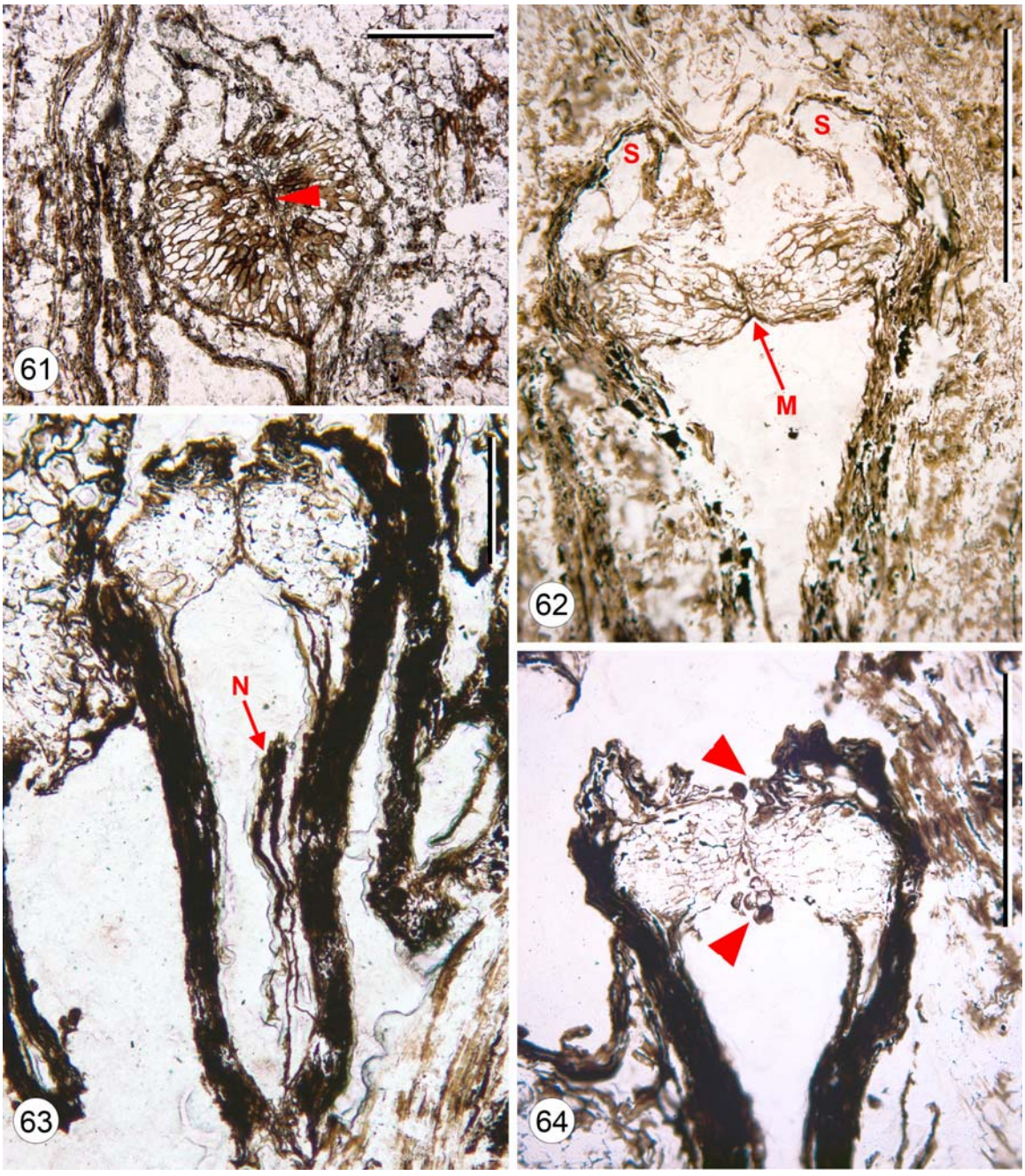
61
S
S
M
62
N
63
64

Plate 18 Fig. 65 *Lakkosia kerasata* gen. et sp. nov. Line drawings of serial sections of the so-called cupulate reproductive structure. Zhao et al. (1995) illustrated sections similar to g and h. The presence of the subtending megasporophyll in oblique section (a–f, grey) indicates that this is part of a multiovulate structure with a laminar megasporophyll and does not have a cupulate morphology. Black dots represent vascular bundles. The dotted lines in g and h indicate the portion of the sporophyll that was not preserved in those sections. These sections show parts of four ovules in serial longitudinal section (numbered), indicating that the ovules were closely packed on the megasporophyll.

a
b
c
d
e
f
g
h
1
2
3
4
65

Plate 19 Figs. 66-71 *Lakkosia kerasata* gen. et sp. nov. Fig. 66: Oblique longitudinal section of an ovule from the specimen described by Taylor and Taylor (1992) showing the sclerotestal pads of tissue (sc) surrounding the micropyle and the remains of the sarcotestal tissue overarching (sa). Holotype slide 7840 (13676 D-bot δ peel 66). scale bar = 0.5 mm. Fig 67: Oblique longitudinal section of an ovule from the specimen described by Zhao et al. (1995) showing the same sclerotestal pads of tissue (sc) and the remains of the overarching sarcotesta (sa). Paratype slide 12925 (13676 D-bot β peel 54). scale bar = 0.5 mm. Fig. 68: Oblique cross section of the megasporophyll (bottom) with part of an ovule in longitudinal section (O), and the thin strips of enclosing tissue originating from the sporophyll (arrows). Holotype slide 7488 (13676 D-bot δ peel 71). scale bar = 0.5 mm. Fig. 69: Oblique longitudinal section of an ovule (O) with the thin strips of tissue from the sporophyll overarching the ovule (arrow). Paratype 13676 E-top series r, peel 48. scale bar = 0.5 mm. Fig. 70: Oblique cross section of the sporophyll (S) showing *Protohaploxypinus* pollen (within circle) between the thin strips of tissue that surround the ovules (arrows). Holotype slide 7837 (13676 D-bot δ peel 59). scale bar = 0.2 mm. Fig. 71: Oblique transverse section of a part of an ovule (O, upper left) showing the thin strips of tissue that partially surround the ovule (arrows). *Protohaploxypinus* pollen occurs between the ovule and the thin strips of tissue (within circle). Paratype slide 23682 (13676 series μ, peel 108). scale bar = 0.2 mm.

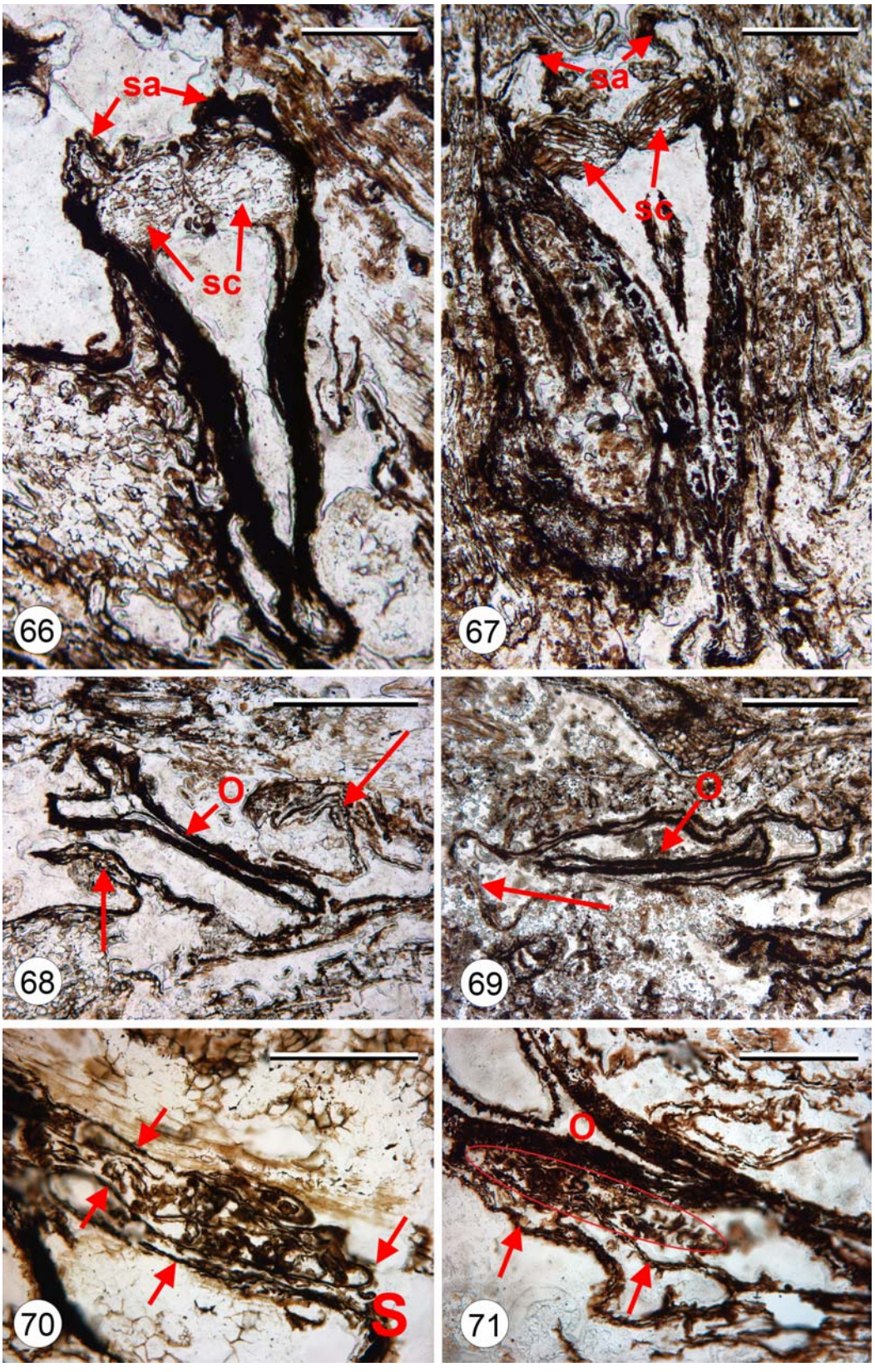
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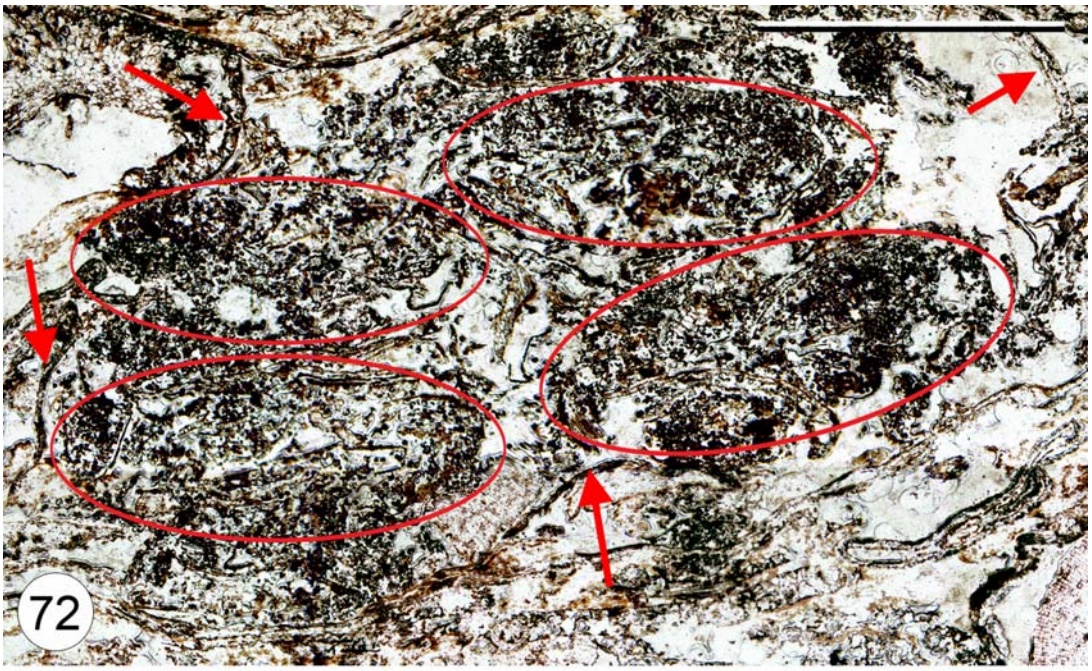
Plate 20 Figs. 72-75 *Arberiella schopfii* sp. nov. Fig. 72: Mass of bisaccate pollen (circles) with remnants of pollen sac walls (arrows) indicating the presence of *Arberiella* in the matrix. Holotype slide 7841 (13676 D-bot δ peel 76). scale bar = 2 mm. Fig. 73: Striations (darker streaks) that run the length of the sporangia from base to apex. Holotype slide 7837 (13676 D-bot δ peel 59). scale bar = 0.2 mm. Fig. 74: *Glossopteris schopfii* leaves (L) associated with the pollen sacs (ps). Holotype slide 7839 (13676 D-bot δ peel 64). scale bar = 0.5 mm. Fig. 75: Pollen sac wall consisting of two cell types. Simple parenchyma cells (pc) in one or two layers make up the majority of the sac wall. Lignified cells (lc) indicate the position of the longitudinal striations on the pollen sac wall. Holotype slide 7838 (13676 D-bot δ peel 60). scale bar = 0.1 mm.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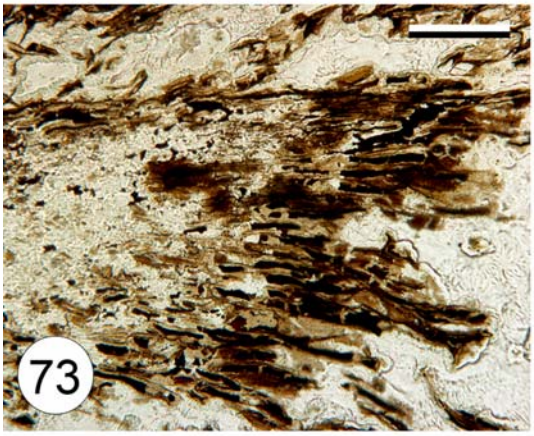
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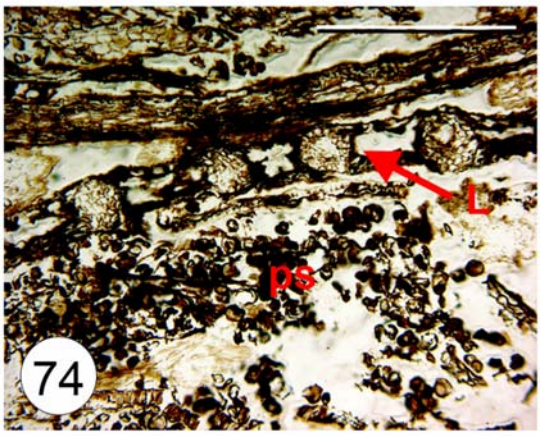
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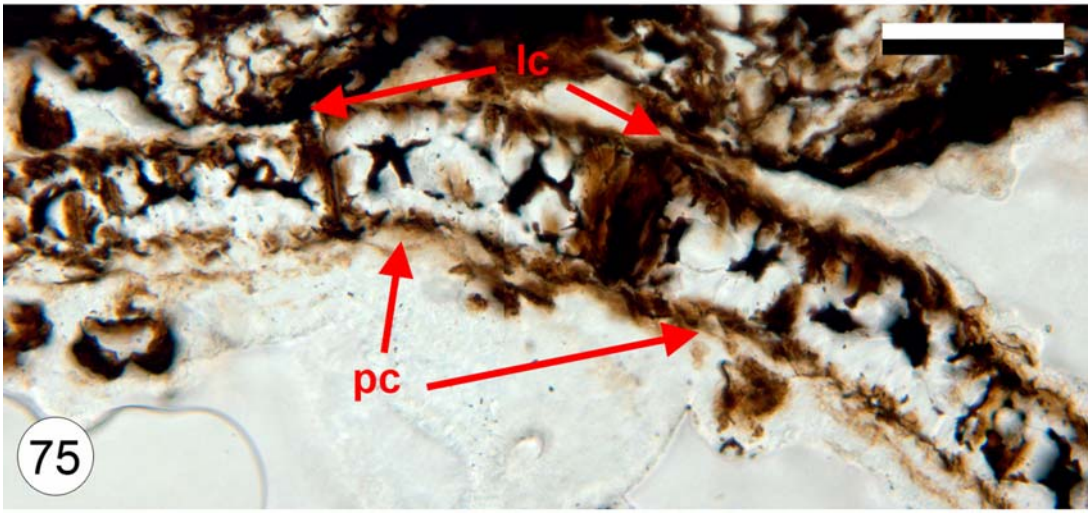
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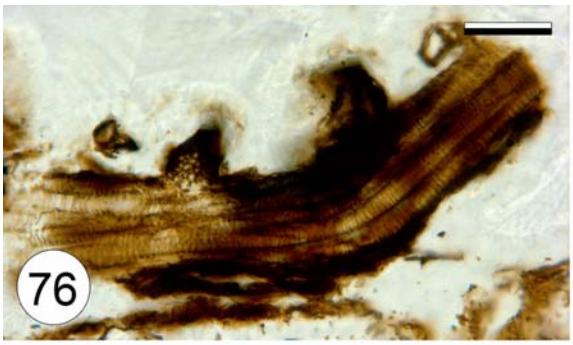
Plate 21 Figs. 76-81. 76-77 *Arberiella schopfii*. Figs. 78-79 *Arberiella* sp. from Australia. Fig. 80 *Eretmonia*. Fig. 81 *Squamella*. Fig. 76: Scalariform tracheids indicating the position of stalks associated with the microsporangia. Holotype slide 7837 (13676 D-bot δ peel 59). scale bar = 0.05 mm. Fig. 77: Bisaccate pollen found within pollen clusters surrounded by microsporangial walls. Endoreticulations can be seen in the sacci. Poor preservation of pollen does not allow for detailed analysis. Holotype slide 13813 (13676 D-bot δ peel 35). scale bar = 0.05 mm. Fig. 78: Permineralized *Arberiella* from Australia showing a collection of pollen sacs. Pollen sacs are more complete in this Australian specimen than in the Antarctic ones, but the preservation of the sporangial wall is not complete enough to determine its cellular composition. Australian Museum Fossil AMFT14698. scale bar = 0.2 mm. Fig. 79: Oblique section of permineralized *Arberiella* from Australia showing pollen contained within the pollen sac indicated by surface striations (dark stripes in image). Pollen in this *Arberiella* is smaller than in *A. schopfii*. Australian Museum Fossil AMFT14698. scale bar = 0.05 mm. Fig. 80: *Eretmonia* sp. from the Late Permian Normandien Formation in South Africa. This specimen typifies *Eretmonia* and shows a scale leaf that normally has a pointed apex (distorted and not easily seen here, blue arrow) and two clusters of sporangia (arrows) near the base of the petiole. Bernard Price Institute Fossil BP-2-8652. scale bar = 1 cm. Fig. 81: *Squamella australis* from the Late Permian Illawarra Coal Measures in Australia. This specimen shows clusters of sporangia (below) attached to a laminar structure (above, with venation) as seen in

other microsporangiate genera of the glossopterids. Australian Museum Fossil AMFT75667. scale bar = 1 mm.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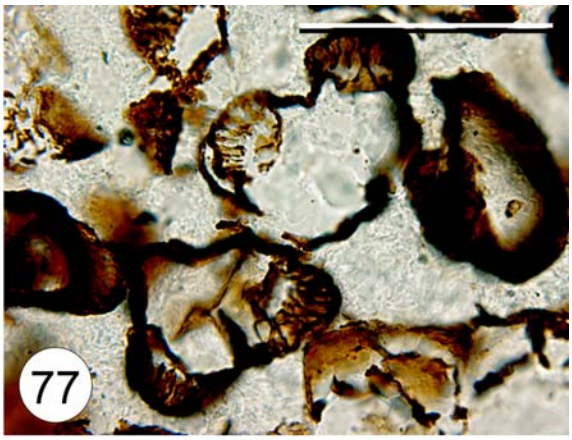
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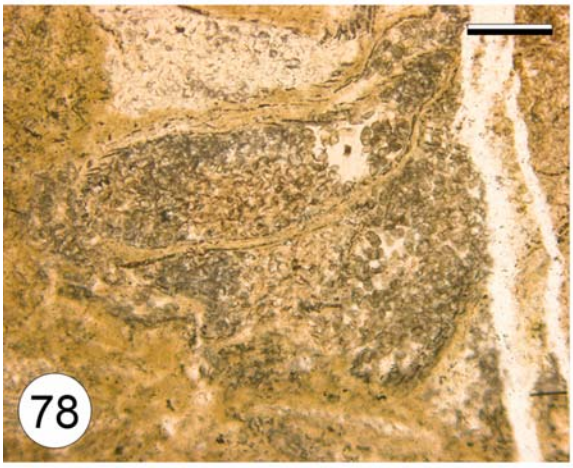
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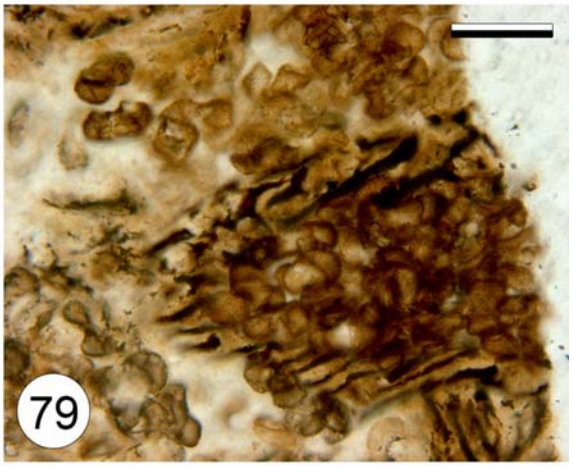
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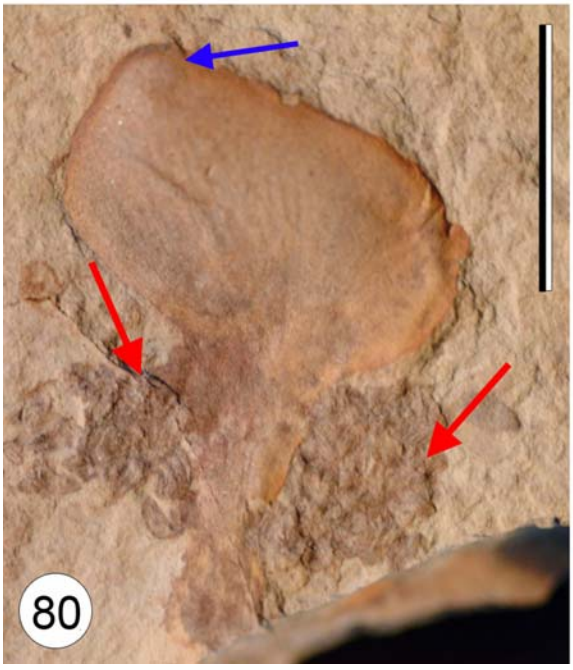
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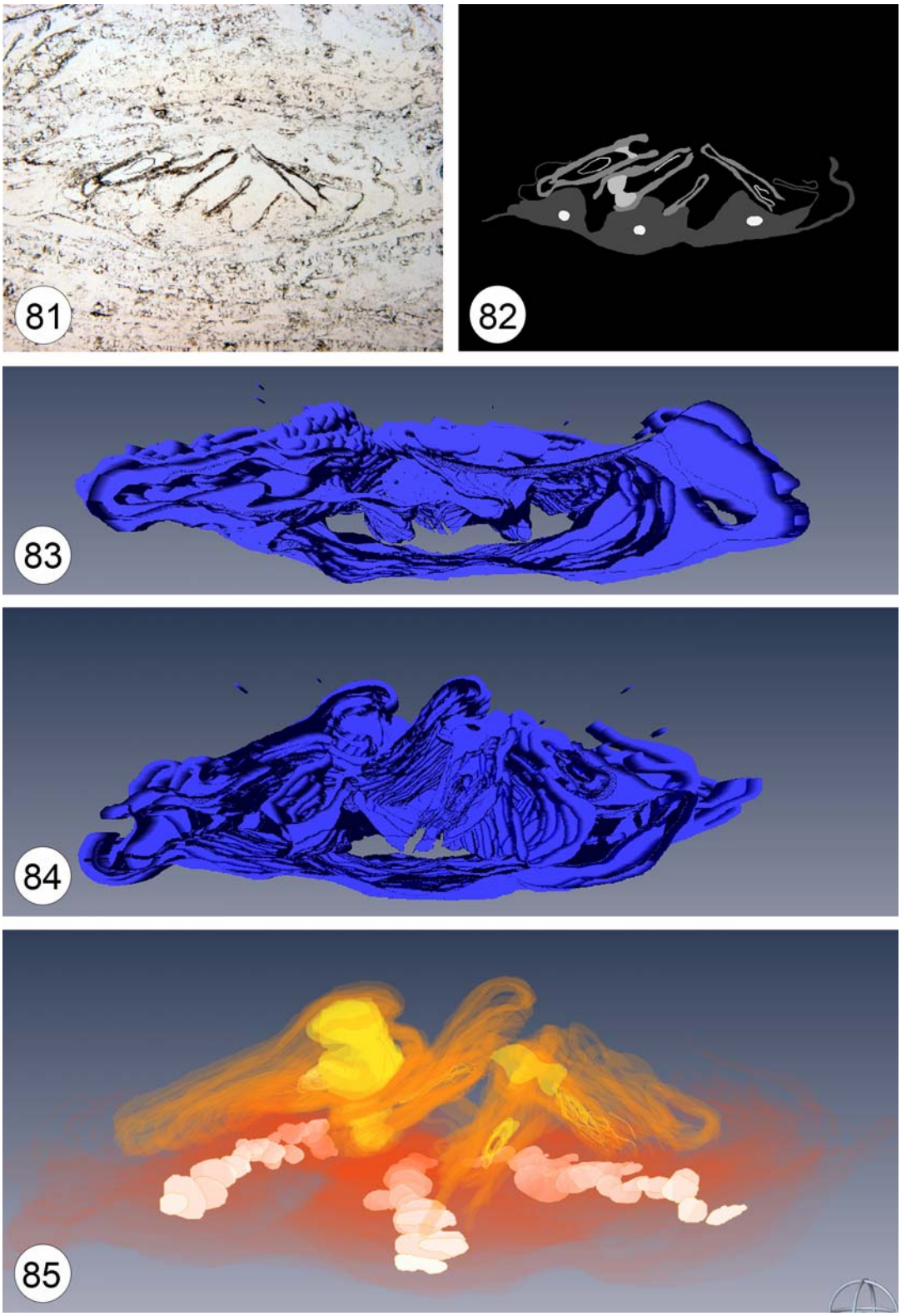
Plate 22 Figs. 81-85 Processing images for 3D reconstruction. Fig. 81: Unprocessed image of the Holotype of *Lakkosia*. KU slide number 13829. scale bar = 1 mm. Fig. 82: Image in figure 1 converted to a greyscale line drawing. Fig. 83: Reconstruction of *Lakkosia* using Amira® software. The view represents the distal edge of the sporophyll looking towards the center. The clear portion in the middle represents the position of the sporophyll. Fig. 84: Reconstruction of *Lakkosia* using Amira® software illustrating the proximal end of the sporophyll looking towards the distal end. The sections of the ovules do not concisely overlap preventing a clear view of what the sporophyll looked like. Fig. 85: *Lakkosia* in Amira® with the overlapping portions of the ovules and sporophyll appearing as darker colors. The more dense the color, the more overlap occurs. Little overlap is seen on the margin of the sporophyll which is represented as a thin red shade. Red = sporophyll, White = vasculature, Orange = ovules, Yellow = micropylar pads.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Appendix A: List of Slides Used for this Study

KU slide #	Previous #	Peel #	Specimen	Genus
	CB451D (B26-a)	26	β series	*Lakkosia* "cupulate" ovule longi section
	CB451D (B27-a)	27	β series	*Lakkosia* "cupulate" ovule longi section
	CB451D (B30-a)	30	β series	*Lakkosia* "cupulate" ovule longi section
	CB451D (B31-a)	31	β series	*Lakkosia* "cupulate" ovule longi section
	CB451D (B32-a)	32	β series	*Lakkosia* "cupulate" ovule longi section
	CB451D (B33-a)	33	β series	*Lakkosia* "cupulate" ovule longi section
	CB451D (B34-a)	34	β series	*Lakkosia* "cupulate" ovule longi section
	CB451D (B35-a)	35	β series	*Lakkosia* "cupulate" ovule longi section
7485	45a	45	δ series	Holotype: *Lakkosia*
7486		93	δ series	Holotype: *Lakkosia*
7488	71a	71	δ series	Holotype: *Lakkosia*
7489	41a	41	δ series	Holotype: *Lakkosia*
7490	50a	50	δ series	Holotype: *Lakkosia*
7491	55a	55	δ series	Holotype: *Lakkosia*
7837	59a	59	δ series	Holotype: *Lakkosia*
7838	60a	60	δ series	Holotype: *Lakkosia*
7839	64a	64	δ series	Holotype: *Lakkosia*
7840	66a	66	δ series	Holotype: *Lakkosia*
7841	76a	76	δ series	Holotype: *Lakkosia*
7842	78a	78	δ series	Holotype: *Lakkosia*
7843	86a	86	β + δ series	Holotype: *Lakkosia*
7844	89a	89	δ series	Holotype: *Lakkosia*
7845		95	δ series	Holotype: *Lakkosia*
7846		96	δ series	Holotype: *Lakkosia*
7847		97	δ series	Holotype: *Lakkosia*
7848		98	δ series	Holotype: *Lakkosia*
7849		99	δ series	Holotype: *Lakkosia*
7850		110	μ series	*Lakkosia* ovule cross section attached to sporophyll
7851		118	μ series	*Lakkosia* ovule cross section attached to sporophyll
7852	78c	78	β series	*Lakkosia* "cupulate" ovule longi section
7854	28a		β2 series	*Lakkosia* ovule cross section attached to sporophyll
7861		47	β series	*Lakkosia* "cupulate" ovule longi section
7877			μ series	*Lakkosia* ovule cross section attached to sporophyll
7878		129	μ series	*Lakkosia* ovule cross section attached to sporophyll
11429		29	β series	*Lakkosia* "cupulate" ovule longi section
12905		25	β series	*Lakkosia* "cupulate" ovule longi section
12906		36	β series	*Lakkosia* "cupulate" ovule longi section
12907		40	β series	*Lakkosia* "cupulate" ovule longi section
12917		41	β series	*Lakkosia* "cupulate" ovule longi section
12918		42	β series	*Lakkosia* "cupulate" ovule longi section
12919		43	β series	*Lakkosia* "cupulate" ovule longi section
12920		44	β series	*Lakkosia* "cupulate" ovule longi section
12921		45	β series	*Lakkosia* "cupulate" ovule longi section
12922		46	β series	*Lakkosia* "cupulate" ovule longi section
12923		47	β series	*Lakkosia* "cupulate" ovule longi section
12924		52	β series	*Lakkosia* "cupulate" ovule longi section
12925		54	β series	*Lakkosia* "cupulate" ovule longi section
12926		57	β series	*Lakkosia* "cupulate" ovule longi section
12927		58	β series	*Lakkosia* "cupulate" ovule longi section

Appendix A: cont.

KU slide #	Previous #	Peel #	Specimen	Genus
12928		59	β series	*Lakkosia* "cupulate" ovule longi section
12938		54	δ series	Holotype
12943		40	δ series	Holotype
13803		14	δ series	*Arberiella*
13804		15	δ series	*Arberiella*
13805		16	δ series	*Arberiella*
13806		17	δ series	*Arberiella*
13807		26	δ series	*Arberiella*
13808		28	δ series	*Arberiella*
13810		31	δ series	*Arberiella*
13811		32	δ series	*Arberiella*
13812		34	δ series	*Arberiella*
13813		35	δ series	*Arberiella*
13814		37	δ series	*Arberiella*
13815		38	δ series	Holotype: *Lakkosia*
13816		39	δ series	Holotype: *Lakkosia*
13817		42	δ series	Holotype: *Lakkosia, Arberiella*
13818		43	δ series	Holotype: *Lakkosia, Arberiella*
13819		44	δ series	Holotype: *Lakkosia, Arberiella*
13820		46	δ series	Holotype: *Lakkosia, Arberiella*
13821		47	δ series	Holotype: *Lakkosia, Arberiella*
13822		48	δ series	Holotype: *Lakkosia, Arberiella*
13823		49	δ series	Holotype
13824		51	δ series	Holotype
13825		52	δ series	Holotype
13826		53	δ series	Holotype
13827		56	δ series	Holotype
13828		57	δ series	Holotype: *Lakkosia, Arberiella*
13829		58	δ series	Holotype
13830		62	δ series	Holotype
13831		63	δ series	Holotype
15682		65	δ series	Holotype: *Lakkosia, Arberiella*
15683		67	δ series	Holotype: *Lakkosia, Arberiella*
15684		69	δ series	Holotype: *Lakkosia, Arberiella*
15685		70	δ series	Holotype: *Lakkosia, Arberiella*
15686		72	δ series	Holotype: *Lakkosia, Arberiella*
15687		73	δ series	Holotype: *Lakkosia, Arberiella*
15688		74	δ series	Holotype: *Lakkosia, Arberiella*
15689		75	δ series	Holotype: *Lakkosia, Arberiella*
15690		77	δ series	Holotype: *Lakkosia, Arberiella*
15691		79	δ series	Holotype: *Lakkosia*
15692		80	δ series	Holotype: *Lakkosia*
15693		81	δ series	Holotype: *Lakkosia*
15694		82	δ series	Holotype: *Lakkosia*
15695		83	δ series	Holotype: *Lakkosia*
15696		87	δ series	Holotype: *Lakkosia*
15697		90	δ series	Holotype: *Lakkosia*
15698		91	δ series	Holotype: *Lakkosia*
15699		92	δ series	Holotype: *Lakkosia*
15700		94	δ series	Holotype: *Lakkosia*
15703		97	δ series	*Arberiella*

Appendix A: cont.

KU slide #	Previous #	Peel #	Specimen	Genus
15704		98	δ series	*Arberiella*
15705		100	δ series	*Arberiella*
15706		101	δ series	*Arberiella*
15707		102	δ series	*Arberiella*
15708		103	δ series	*Arberiella*
15709		104	δ series	*Arberiella*
15710		106	δ series	*Arberiella*
15711		108	δ series	*Arberiella*
15713		111	δ series	*Lakkosia* ovule cross section attached to sporophyll
15714		114	δ series	*Lakkosia* ovule cross section attached to sporophyll
15716		117	δ series	*Arberiella*
15717		119	δ series	*Arberiella*
15718		120	δ series	*Arberiella*
15719		121	δ series	*Arberiella*
15720		122	δ series	*Lakkosia* ovule cross section attached to sporophyll
15821		123	δ series	*Arberiella*
15724		48	β series	*Lakkosia* "cupulate" ovule longi section
15725		62	β series	*Lakkosia* "cupulate" ovule longi section
15726		64	β series	*Lakkosia* "cupulate" ovule longi section
15727		65	β series	*Lakkosia* "cupulate" ovule longi section
15728		66	β series	*Lakkosia* "cupulate" ovule longi section
15729		70	β series	*Lakkosia* "cupulate" ovule longi section
15730		71	β series	*Lakkosia* "cupulate" ovule longi section
15731		75	β series	*Lakkosia* "cupulate" ovule longi section
15732		77	β series	*Lakkosia* "cupulate" ovule longi section
15733		79	β series	*Lakkosia* "cupulate" ovule longi section
15734		80	β series	*Lakkosia* "cupulate" ovule longi section
15735		81	β series	*Lakkosia* "cupulate" ovule longi section
15736		83	β series	*Lakkosia* "cupulate" ovule longi section
15737		85	β series	*Lakkosia* "cupulate" ovule longi section
15739		101	β2 series	*Lakkosia* "cupulate" ovule longi section
15740		107	β2 series	*Lakkosia* "cupulate" ovule longi section
15741		108	β2 series	*Lakkosia* "cupulate" ovule longi section
15743		110	β2 series	*Lakkosia* "cupulate" ovule longi section
15744		112	β2 series	*Lakkosia* "cupulate" ovule longi section
15757		129	δ series	*Arberiella*
15760		43	δ2 series	*Arberiella*
15761		49	δ2 series	*Arberiella*
15762		52	δ2 series	*Arberiella*
15763		56	δ2 series	*Arberiella*
15764		62	δ2 series	*Arberiella*
15765		90	δ2 series	*Arberiella*
15766		95	δ2 series	*Arberiella*
15767		96	δ2 series	*Arberiella*
15768		114	δ2 series	*Lakkosia* ovule cross section attached to sporophyll
15769		115	δ2 series	*Lakkosia* ovule cross section attached to sporophyll
15770		117	δ2 series	*Lakkosia* ovule cross section attached to sporophyll
15771		118	δ2 series	*Arberiella*
15773		120	μ series	*Lakkosia* ovule cross section attached to sporophyll
15774		121	δ2 series	*Lakkosia* ovule cross section attached to sporophyll
15776		128	δ2 series	*Arberiella*

Appendix A: cont.

KU slide #	Previous #	Peel #	Specimen	Genus
15777		129	δ2 series	*Lakkosia* ovule cross section attached to sporophyll
23667	CB451D (B26-a)	26	β2 series	*Lakkosia* ovule cross section attached to sporophyll
23668	CB451D (B27-a)	27	β2 series	*Lakkosia* ovule cross section attached to sporophyll
23669	CB451D (B30-a)	30	β2 series	*Lakkosia* ovule cross section attached to sporophyll
23670	CB451D (B31-a)	31	β2 series	*Lakkosia* ovule cross section attached to sporophyll
23671	CB451D (B32-a)	32	β2 series	*Lakkosia* ovule cross section attached to sporophyll
23672	CB451D (B33-a)	33	β2 series	*Lakkosia* ovule cross section attached to sporophyll
23673	CB451D (B34-a)	34	β2 series	*Lakkosia* ovule cross section attached to sporophyll
23674	CB451D (B35-a)	35	β2 series	*Lakkosia* ovule cross section attached to sporophyll
23675	CB451D (B-100a)	100	μ series	*Lakkosia* ovule cross section attached to sporophyll
23676	CB451D (B-105a)	105	μ series	*Lakkosia* ovule cross section attached to sporophyll
23677		101	μ series	*Lakkosia* ovule cross section attached to sporophyll
23678		102	μ series	*Lakkosia* ovule cross section attached to sporophyll
23679		104	μ series	*Lakkosia* ovule cross section attached to sporophyll
23680		106	μ series	*Lakkosia* ovule cross section attached to sporophyll
23681		107	μ series	*Lakkosia* ovule cross section attached to sporophyll
23682		108	μ series	*Lakkosia* ovule cross section attached to sporophyll
23683		112	μ series	*Lakkosia* ovule cross section attached to sporophyll
23684		113	μ series	*Lakkosia* ovule cross section attached to sporophyll
23685		126	μ series	*Lakkosia* ovule cross section attached to sporophyll
23686		127	μ series	*Lakkosia* ovule cross section attached to sporophyll
23687		24	β series	*Lakkosia* "cupulate" ovule longi section
23688		37	β series	*Lakkosia* "cupulate" ovule longi section
23689		38	β series	*Lakkosia* "cupulate" ovule longi section
23690		39	β series	*Lakkosia* "cupulate" ovule longi section
23691		41	β series	*Lakkosia* "cupulate" ovule longi section
23692		51	β series	*Lakkosia* "cupulate" ovule longi section
23693		53	β series	*Lakkosia* "cupulate" ovule longi section
23694		55	β series	*Lakkosia* "cupulate" ovule longi section
23695		56	β series	*Lakkosia* "cupulate" ovule longi section
23696		63	β series	*Lakkosia* "cupulate" ovule longi section
23697		67	β series	*Lakkosia* "cupulate" ovule longi section
23698		68	β series	*Lakkosia* "cupulate" ovule longi section
23699		69	β series	*Lakkosia* "cupulate" ovule longi section
23700		72	β series	*Lakkosia* "cupulate" ovule longi section
23701		73	β series	*Lakkosia* "cupulate" ovule longi section
23702		74	β series	*Lakkosia* "cupulate" ovule longi section
23703		76	β series	*Lakkosia* "cupulate" ovule longi section
23704		82	β series	*Lakkosia* "cupulate" ovule longi section
23705		84	β series	*Lakkosia* "cupulate" ovule longi section
23706		86	β series	*Lakkosia* "cupulate" ovule longi section
23707		87	β series	*Lakkosia* "cupulate" ovule longi section
23708		88	β series	*Lakkosia* "cupulate" ovule longi section
23709		89	β series	*Lakkosia* "cupulate" ovule longi section
23710		90	β series	*Lakkosia* "cupulate" ovule longi section
23711		91	β series	*Lakkosia* "cupulate" ovule longi section
23712		92	β series	*Lakkosia* "cupulate" ovule longi section
23713		93	β series	*Lakkosia* "cupulate" ovule longi section
23714		94	β series	*Lakkosia* "cupulate" ovule longi section
23715		95	β series	*Lakkosia* "cupulate" ovule longi section

Appendix A: cont.

KU slide #	Previous #	Peel #	Specimen	Genus
23716		96	β series	*Lakkosia* "cupulate" ovule longi section
23717		98	β series	*Lakkosia* "cupulate" ovule longi section
23718		61	δ series	*Lakkosia* Holotype
23719		68	δ series	*Lakkosia* Holotype
23720		61	β series	*Lakkosia* "cupulate" ovule longi section
23721		24	δ2 series	*Arberiella*
23722		25	δ2 series	*Arberiella*
23723		27	δ2 series	*Arberiella*
23724		29	δ2 series	*Arberiella*
23725		30	δ2 series	*Arberiella*
23726		36	δ2 series	*Arberiella*
23727		53	δ2 series	*Arberiella*
23728		58	δ2 series	*Arberiella*
23729		61	δ2 series	*Arberiella*
23730		73	δ2 series	*Arberiella*
23731		79	δ2 series	*Arberiella*
23732		91	δ2 series	*Arberiella*
23733		92	δ2 series	*Arberiella*
23734		99	δ2 series	*Arberiella*
23735		105	δ2 series	*Arberiella*
23736		112	δ2 series	*Arberiella*
23737		113	δ2 series	*Arberiella*
23738		116	δ2 series	*Arberiella*
23739		118	δ2 series	*Arberiella*
23740		122	δ2 series	*Arberiella*
23741		124	δ2 series	*Arberiella*
23742		125	δ2 series	*Arberiella*
23743		126	δ2 series	*Arberiella*
23744		127	δ2 series	*Arberiella*
26374		11	q series	*Lakkosia*
26375		12	q series	*Lakkosia*
26376		13	q series	*Lakkosia*
26377		14	q series	*Lakkosia*
26378		15	q series	*Lakkosia*
26379		16	q series	*Lakkosia*
26380		17	q series	*Lakkosia*
26381		18	q series	*Lakkosia*
26382		19	q series	*Lakkosia*
26383		20	q series	*Lakkosia*
26384		21	q series	*Lakkosia*
26385		22	q series	*Lakkosia*
26386		23	q series	*Lakkosia*
26387		24	q series	*Lakkosia*
26388		25	q series	*Lakkosia*
26389		26	q series	*Lakkosia*
26390		27	q series	*Lakkosia*
26391		28	q series	*Lakkosia*
26392		29	q series	*Lakkosia*
26393		30	q series	*Lakkosia*
26394		31	q series	*Lakkosia*

Appendix A: cont.

KU slide #	Previous #	Peel #	Specimen	Genus
26395		32	q series	*Lakkosia*
26396		33	q series	*Lakkosia*
26397		34	q series	*Lakkosia*
26398		35	q series	*Lakkosia*
26399		39	q series	*Lakkosia*
26400		40	q series	*Lakkosia*
26401		41	q series	*Lakkosia*
26402		42	q series	*Lakkosia*
26403		43	q series	*Lakkosia*
26404		44	q series	*Lakkosia*
26405		45	q series	*Lakkosia*
26406		46	q series	*Lakkosia*
26407		47	q series	*Lakkosia*
26408		48	q series	*Lakkosia*
26409		49	q series	*Lakkosia*
26410		53	q series	*Lakkosia*
26411		54	q series	*Lakkosia*
26412		55	q series	*Lakkosia*
26413		56	q series	*Lakkosia*
26414		57	q series	*Lakkosia*
26415		58	q series	*Lakkosia*
26416		59	q series	*Lakkosia*
26417		60	q series	*Lakkosia*
26418		61	q series	*Lakkosia*
26419		63	q series	*Lakkosia*
26420		64	q series	*Lakkosia*
26421		65	q series	*Lakkosia*
26422		66	q series	*Lakkosia*
26423		67	q series	*Lakkosia*
26424		68	q series	*Lakkosia*
26425		69	q series	*Lakkosia*
26426		71	q series	*Lakkosia*
26427		75	q series	*Lakkosia*
26428		76	q series	*Lakkosia*
26429		38	p series	*Lakkosia*
26430		39	p series	*Lakkosia*
26431		40	p series	*Lakkosia*
26432		41	p series	*Lakkosia*
26433		42	p series	*Lakkosia*
26434		43	p series	*Lakkosia*
26435		46	p series	*Lakkosia*
26436		48	p series	*Lakkosia*
26437		49	p series	*Lakkosia*
26438		50	p series	*Lakkosia*
26439		7	r series	*Lakkosia*
26440		8	r series	*Lakkosia*
26441		9	r series	*Lakkosia*
26442		10	r series	*Lakkosia*
26443		11	r series	*Lakkosia*
26444		12	r series	*Lakkosia*
26445		13	r series	*Lakkosia*

Appendix A: cont.

KU slide #	Previous #	Peel #	Specimen	Genus
26446		14	r series	*Lakkosia*
26447		15	r series	*Lakkosia*
26448		16	r series	*Lakkosia*
26449		17	r series	*Lakkosia*
26450		18	r series	*Lakkosia*
26451		19	r series	*Lakkosia*
26452		20	r series	*Lakkosia*
26453		21	r series	*Lakkosia*
26454		22	r series	*Lakkosia*
26455		23	r series	*Lakkosia*
26456		24	r series	*Lakkosia*
26457		25	r series	*Lakkosia*
26458		26	r series	*Lakkosia*
26459		27	r series	*Lakkosia*
26460		28	r series	*Lakkosia*
26461		29	r series	*Lakkosia*
26462		30	r series	*Lakkosia*
26463		31	r series	*Lakkosia*
26464		32	r series	*Lakkosia*
26465		33	r series	*Lakkosia*
26466		34	r series	*Lakkosia*
26467		35	r series	*Lakkosia*
26468		39	r series	*Lakkosia*
26469		41	r series	*Lakkosia*
26470		42	r series	*Lakkosia*
26471		43	r series	*Lakkosia*
26472		44	r series	*Lakkosia*
26473		45	r series	*Lakkosia*
26474		47	r series	*Lakkosia*
26475		48	r series	*Lakkosia*
26476		49	r series	*Lakkosia*
26477		53	r series	*Lakkosia*
26478		54	r series	*Lakkosia*
26479		55	r series	*Lakkosia*
26480		57	r series	*Lakkosia*
26481		58	r series	*Lakkosia*
26482		59	r series	*Lakkosia*
26483		60	r series	*Lakkosia*
26484		61	r series	*Lakkosia*
26485		62	r series	*Lakkosia*
26486		63	r series	*Lakkosia*
26487		64	r series	*Lakkosia*
26488		65	r series	*Lakkosia*
26489		66	r series	*Lakkosia*
26490		67	r series	*Lakkosia*
26491		68	r series	*Lakkosia*
26492		69	r series	*Lakkosia*
26493		71	r series	*Lakkosia*
26494		75	r series	*Lakkosia*
26495		76	r series	*Lakkosia*
26496		56	r series	*Lakkosia*

Appendix A: cont.

AUST slide #	Previous #	Peel #	Specimen	Genus
AMFt14524				*Homevaleia*
AMFt14525				*Homevaleia*
AMFt14526				*Homevaleia ovules*
AMFt14527				*Homevaleia*
AMFt14528				*Homevaleia ovules*
AMFt14529				*Homevaleia*
AMFt14530				*Homevaleia ovules*
AMFt14531				*Homevaleia*
AMFt14532				*Homevaleia*
AMFt14533				*Homevaleia*
AMFt14534				*Homevaleia*
AMFt14535				*Homevaleia*
AMFt14536				*Homevaleia*
AMFt14537				*Homevaleia ovules*
AMFt14538				*Homevaleia*
AMFt14539				*Homevaleia ovules*
AMFt14540				*Homevaleia*
AMFt14541				*Homevaleia*
AMFt14609				*Homevaleia ovules*
AMFt14641				*Homevaleia ovules*
AMFt14663				*Homevaleia*
AMFt14673	UNEF15279; UNEF15280; UNEF15283			*Homevaleia*
AMFt14674	UNEF15276			*Homevaleia*
AMFt14677	UNEF15286			*Homevaleia*
AMFt14678	UNEF15278; UNEF15285			*Homevaleia ovules*
AMFt14679	UNEF15296			*Homevaleia*
AMFt14680	UNEF15280			*Homevaleia*
AMFt14681	UNEF15297; UNEF15298			*Homevaleia*
AMFt14682	UNEF15296			*Homevaleia*
AMFt14683	UNEF15276; UNEF15299			*Homevaleia*
AMFt14684	UNEF15276; UNEF15299			*Homevaleia*
AMFt14685	UNEF15276; UNEF15299			*Homevaleia*
AMFt14686	UNEF15276; UNEF15299			*Vertebraria*
AMFt14687	UNEF15281			*Homevaleia*
AMFt14688	UNEF15279; UNEF15280; UNEF15283			*Homevaleia*
AMFt14689	UNEF15286			*Homevaleia*
AMFt14690	UNEF15278; UNEF15285			*Homevaleia*
AMFt14691	UNEF15282			*Homevaleia*
AMFt14692	UNEF15284			*Homevaleia*
AMFt14693	UNEF15287			*Homevaleia*
AMFt14694	UNEF15282; 15290			*Homevaleia*
AMFt14695	UNEF15292			*Homevaleia*
AMFt14698	UNEF15296			*Arberiella*
AMFt14699	UNEF15300			*Homevaleia*; *Arberiella*
AMFt14700	UNEF15301			*Homevaleia* ovules
AMFt14701	UNEF15288; UNEF15302			*Homevaleia*
AMFt14702	UNEF15293; UNEF15303			*Homevaleia*
AMFt15295	UNEF15295			*Homevaleia*
	UNEF15302; UNEF15304; UNEF15291			*Homevaleia*